

GROWTH RATES OF CALANOID COPEPODS IN THE NORTHERN GULF OF  
ALASKA, AND THEIR RELATIONSHIPS TO TEMPERATURE, CHLOROPHYLL  
AND BODY SIZE

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By

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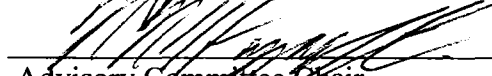
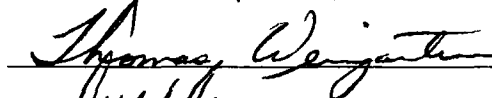
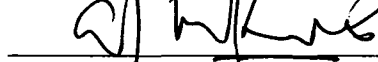
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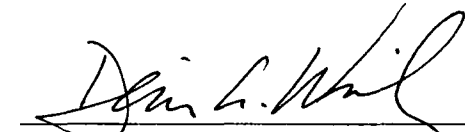


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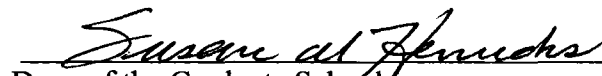


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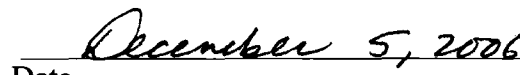
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## ABSTRACT

The juvenile growth rate and development time of the dominant calanoid copepods in the northern Gulf of Alaska were investigated. The utility of the artificial-cohort method was successfully validated as the most practical approach for estimating copepod growth rates in this ecosystem. The underlying functional responses of growth rates to temperature, food concentration, and body size were thoroughly explored for *Neocalanus flemingeri/plumchrus*, *Metridia pacifica*, *Calanus marshallae*, *C. pacificus* and *Pseudocalanus* spp. These results lay the foundation for the calculation of copepod secondary production and ongoing ecosystem modeling activities for the northern Gulf of Alaska, and will contribute to the refinement of global models of copepod growth rates.

In general, the rates of copepod growth were negatively size-dependent. However, a positive relationship between growth rate and body size within each stage emerged in response to food climate. The effect of temperature on growth rates was prominent, but confounded with food conditions and body sizes, which also vary with temperature conditions. Copepod growth rates were significantly related to chlorophyll *a*, and were frequently food-limited, particularly for later developmental stages during the summer. Compared to other co-occurring calanoid copepods, egg-carrying species (i.e. *Pseudocalanus*) tend to grow slowly to meet their unique life history strategy. Statistically, more variability in temperature corrected growth rates can be explained by composite nonlinear models that incorporate development stage and body size into the traditional Michaelis-Menten relationship. The species-specific comparisons of the measured growth rates with those predicted by global models of copepod growth suggested more direct measurements of copepod growth rates in various ecosystems are required for fully appreciating the global patterns of copepod growth. Caution should be used in the widespread application of those models for estimating copepod secondary production, especially in polar and sub-polar waters.

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## GENERAL INTRODUCTION

As grazers and nutrient recyclers, zooplankton play a key role in marine ecosystems by controlling phytoplankton production and shaping pelagic food webs (Kiørboe, 1997). Copepods account for up to 80% of the mesozooplankton biomass in the world's oceans and are considered a particularly successful group in pelagic environments (Verity and Smetacek, 1996). The majority of more than 8500 known species of copepods live in marine ecosystems, although they also occur in vast numbers in fresh water environments. Taxonomically, the calanoid copepods comprise the majority of planktonic zooplankton in the world's oceans (Mauchline, 1998).

The coastal Gulf of Alaska supports a highly diverse ecosystem, and sustains numerous species of fishes, marine mammals and sea birds (Weingartner *et al.*, 2002). In this region, calanoid copepods are the numerically most abundant component of the zooplankton community (Incze *et al.*, 1997; Coyle and Pinchuk 2003, 2005). In recent decades, our knowledge of zooplankton communities in this area has improved considerably. We now know the important players in the zooplankton communities and their overall life histories in the Gulf of Alaska (Miller *et al.*, 1984; Incze *et al.*, 1997; Coyle and Pinchuk 2003, 2005). Nonetheless, our knowledge of copepod population dynamics is largely inferred from examination of preserved collections (natural cohort analysis). Prior to the studies discussed in this dissertation, there were only a few direct measurements of growth and development for dominant copepod species in the Gulf of Alaska (Fulton, 1973; Miller and Nielsen, 1988). Moreover, the relationship between copepod growth and environmental variables in this area was unclear.

Over the past few decades copepod productivity has become a central aspect of marine plankton research (Poulet *et al.*, 1995; Runge and Roff, 2000). However, without precisely measured copepod rate processes our understanding of the trophodynamics of the marine ecosystem will remain incomplete (Longhurst, 1984). While various methods have been available for the routine measurement of primary production, until now no specific method has been routinely utilized for measuring secondary production in marine ecosystems. Generally, for a given species, secondary production is calculated from the



product of specific growth rate and biomass (Poulet *et al.*, 1995; Runge and Roff, 2000). Advances in biological oceanographic instrumentation (see Wiebe and Benfield, 2003) have improved the availability of time- and site-specific data on zooplankton composition, abundance and biomass in the ocean. Thus, *in situ* growth rates are the bottleneck to precisely calculating secondary production in marine ecosystems.

Growth is a key component of the physiological process of marine metazoans because an individual's growth amounts to the net result of all physiological and behavioral processes, i.e. grazing, assimilation, respiration, excretion and reproduction (Hopcroft, 1997). How zooplankton respond to their nutritional environment may provide insights on whether the food source (i.e. bottom-up control) is the main process regulating the population growth of zooplankton, or if predation (i.e. top-down control) is more important (Hunt and McKinnell, 2006). Clearly, such knowledge is vital in fully appreciating the roles of copepods in shaping the structure of marine ecosystems. Moreover, our understanding of the functional relationships between growth rates and environmental factors (e.g., temperature, chlorophyll *a* and body size) assists the global synthesis of copepod growth rates (e.g., Huntley and Lopez, 1992; Hirst and Lampitt, 1998; Hirst and Bunker, 2003; Hirst *et al.*, 2003; Bunker and Hirst, 2004), and is required for modeling ecosystems.

Methodologically, two demographic approaches have been employed for studying copepod growth and production in the field, i.e. the “natural cohort” and “artificial cohort” approaches (Runge and Roff, 2000). However, each approach has pros and cons, and involves tradeoffs between biases and practicality (Kimmerer *et al.*, in press). Traditionally, egg production has been considered as a proxy for growth rate of juvenile developmental stages, based on the assumption that adult copepods cease somatic growth and that equivalent growth continues as egg production (e.g., Sekiguchi *et al.*, 1980; Runge and Roff, 2000). Increasingly, this assumption has proven inaccurate (e.g., Peterson *et al.*, 1991; Hopcroft and Roff, 1998; Hirst and McKinnon, 2001).

Regardless of which method is utilized, estimating *in situ* growth rates is a daunting task due to its time consuming and labor intensive nature. The lack of directly measured

growth rates also fosters the widespread use of global models of copepod growth. Unfortunately these models have often been proven unsatisfactory (Richardson *et al.*, 2001; Peterson *et al.*, 2002; Rey-Rassalt *et al.*, 2004). At present, our knowledge of copepod growth rates in nature has been predominantly limited to tropical and temperate waters. In subpolar and polar waters, there is a conspicuous deficiency of data on juvenile copepod growth despite the abundant information on egg production rates (see Hirst and Bunker, 2003), and there are virtually no measurements of vital rates for the common copepod species characteristic of the entire subarctic Pacific.

The theme of this study, to determine growth rates of the dominant zooplankton and their functional responses to environmental variables in the northern Gulf of Alaska, is challenging. The dynamic physical and biological conditions (advective features, temperature and food conditions) test existing techniques and strain available manpower. The selected target species, i.e., *Neocalanus flemingeri/plumchrus*, *Metridia pacifica*, *Calanus marshallae*, *C. pacificus* and *Pseudocalanus* spp., include both oceanic and neritic species with a range of body sizes and reproductive characteristics (i.e. broadcast, egg-carrying). As ecologically important players, they account for up to 75% of total annual secondary production in this ecosystem (Coyle and Pinchuk, 2003). This is the first comprehensive study of multi-species key rate processes to explain the integrated functioning of this productive planktonic system in the northern Gulf of Alaska.

The objectives of this dissertation are to: (1) validate the utility of the artificial-cohort method as the most practical approach for estimating growth rates of copepods at the community level in subarctic Pacific waters; (2) provide vital process data (i.e., development time, growth rates) of key Gulf of Alaska species, i.e., *Neocalanus flemingeri/plumchrus*, *Metridia pacifica*, *Calanus marshallae*, *C. pacificus* and *Pseudocalanus* spp., for the synthesis study of this ecosystem; (3) explore the functional responses of growth rates to environmental factors (i.e., food resource, temperature and body size); (4) test the generality of the global models of copepod growth rates for species in this system and develop local empirical models for precise predictions of growth rates of copepods.

This dissertation is written following the copepod species in reverse order of body size, with certain topics emphasized separately for each chapter. In Chapter 1, I demonstrate the utility of the “artificial cohort” method through comparison to the concurrent experiments by the single-stage method for the largest copepods, i.e., *Neocalanus flemingeri/plumchrus*. In addition to examining food-limited growth through food enhancement experiments, I also explore the relationship between growth rates and body size within each single stage. In Chapter 2, I explore the relationship between growth rates and body size for *Metridia pacifica*, and demonstrate the confounding effect of food and body size through the development of a composite model. In Chapter 3, I compare the seasonal variability in growth rates of *Calanus marshallae* and *C. pacificus*, and investigate their response to food conditions. Chapter 4 provides the first field results on growth rates of *Pseudocalanus* species, and compares egg-carrying copepods to other larger broadcast species in this area. In addition to examining seasonal variations in the growth rates and functional relationships to other environmental variables, I compare the utility of the composite model for dominant copepods in this area. Finally, I summarize the general conclusions in this dissertation and give suggestions for future related research.

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## ***Chapter 1***

### **Growth and development of *Neocalanus flemingeri/plumchrus* in the northern Gulf of Alaska: validation of the artificial cohort method in cold waters\***

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## ABSTRACT

*In situ* growth and development of *Neocalanus flemingeri/plumchrus* stage C1–C4 copepodites were estimated by both the artificial-cohort and the single-stage incubation methods in March, April and May of 2001–2005 at 5–6°C. Results from these two methods were comparable and consistent. In the field, C1–C4 stage durations ranged from 7 to >100 days, dependent on temperature and chlorophyll *a* (Chl *a*) concentration. Average stage durations were 12.4–14.1 days, yielding an average of 56 days to reach C5, but under optimal conditions stage durations were closer to 10 days, shortening the time to reach C5 (from C1) to 46 days. Generally, growth rates decreased with increasing stage, ranging from 0.28 day<sup>-1</sup> to close to zero but were typically between 0.20 and 0.05 day<sup>-1</sup>, averaging 0.110±0.006 day<sup>-1</sup> (mean±SE) for single-stage and 0.107±0.005 day<sup>-1</sup> (mean±SE) for artificial-cohort methods. Growth was well described by equations of Michaelis–Menten form, with maximum growth rates ( $G_{\max}$ ) of 0.17–0.18 day<sup>-1</sup>, and half saturation Chl *a* concentrations ( $K_{\text{chl}}$ ) of 0.45–0.46 mg m<sup>-3</sup> for combined C1–3, while  $G_{\max}$  dropped to 0.08–0.09 day<sup>-1</sup> but  $K_{\text{chl}}$  remained at 0.38–0.93 mg m<sup>-3</sup> for C4. In this study, *in situ* growth of *N. flemingeri/plumchrus* was frequently food limited to some degree, particularly during March. A comparison with global models of copepod growth rates suggests that these models still require considerable refinement. We suggest that the artificial-cohort method is the most practical approach to generating the multispecies data required to address these deficiencies.

**Key words:** *Neocalanus*, growth, development, artificial-cohort, subarctic



## INTRODUCTION

As grazers and nutrient recyclers, copepods play an important role in marine ecosystems linking primary production to upper trophic levels and accounting for up to 80% of the metazoan biomass in the marine environment (Kiørboe, 1998). Over the last few decades, copepod productivity has become a major focus of research necessitating precise measurement of copepod rate processes to fully understand the trophodynamics of marine ecosystems (Longhurst, 1984). Traditionally, egg production has been considered an easy and quick proxy for growth rate of all developmental stages, based on the assumption that adult copepods cease somatic growth and that equivalent growth continues as egg production (Sekiguchi *et al.*, 1980; Berggreen *et al.*, 1988; Runge and Roff, 2000). Increasingly, this assumption has been challenged (Peterson *et al.*, 1991; Hutchings *et al.*, 1995; Hopcroft and Roff, 1998; Richardson *et al.*, 1998; Calbet *et al.*, 2000; Hirst and McKinnon, 2001). At present, our knowledge of somatic growth is incomplete, despite recent attempts at synthesis (Hopcroft *et al.*, 1998; Hirst and Lampitt, 1998; Hirst and Bunker, 2003). This lack of knowledge is greatest for cold waters and particularly for species in the subarctic North Pacific.

Within the subarctic North Pacific, *Neocalanus* spp. are a major component of the seasonal zooplankton cycle (Miller, 1993; Mackas and Tsuda, 1999; Coyle and Pinchuk, 2003, 2005). Their abundance and large size make *Neocalanus* spp. an important prey species for many higher trophic levels (e.g. Kawamura, 1982; Willette *et al.*, 1999; Moku *et al.*, 2000; Hunter *et al.*, 2002) especially for the productive salmon fisheries in the Gulf of Alaska (Weingartner *et al.*, 2002; Armstrong *et al.*, 2005; Cross *et al.*, 2005). Each of the three species, *Neocalanus plumchrus*, *Neocalanus flemingeri* and *Neocalanus cristatus*, exhibits extensive ontogenetic vertical migrations and diapause in deep water over the winter. During early spring, they grow and develop in the surface layer while feeding on phytoplankton and microzooplankton (Dagg, 1993; Gifford, 1993). Their reproductive maturation and egg production take place in the deeper layers (>250m) without feeding (Miller *et al.*, 1984; Miller and Clemons, 1988). *Neocalanus flemingeri* and *N. plumchrus* are more abundant and common within the upper mixed layer (Miller,

1988; Coyle and Pinchuk, 2005) than *N. cristatus* and clearly divide the surface mixing layer seasonally (Mackas *et al.*, 1993). Temporally, the newly recruited copepodites of *N. flemingeri* are observed in the surface mixed layer earlier in spring than those of *N. plumchrus* (Tsuda *et al.*, 1999). Spatially, *N. flemingeri* is more common within inner-shelf waters on the northern Gulf of Alaska shelf than the other two species (Coyle and Pinchuk, 2005).

While we have an overall picture of the life cycle of *N. flemingeri* and *N. plumchrus* from numerous studies in the subarctic Pacific, few direct estimates of their vital rates exist. We are limited to the single-stage method determined rates of C4 (duration) and C5 (growth) copepodites of *N. plumchrus* (Miller and Nielsen, 1988); natural cohort growth rates of C1–C5 copepodites of *N. cristatus* and *N. plumchrus/flemingeri* (Vidal and Smith, 1986); laboratory rates for C2–C4 copepodites of *N. flemingeri* (Slater and Hopcroft, in review) and three studies of egg production and naupliar development of *N. cristatus*, *N. flemingeri* and/or *N. plumchrus* (Fulton, 1973; Saito and Tsuda, 2000; Slater and Hopcroft, in review). Despite their importance, *in situ* somatic growth rates for younger copepodites of *N. flemingeri* are unavailable.

In the coastal Gulf of Alaska, it is generally difficult to track natural cohorts due to the region's highly advective nature and the high sampling frequency required for robust estimates (Miller and Clemons, 1988; Miller and Nielsen, 1988; Miller, 1993). Alternatively, "single-stage" and "artificial-cohorts" incubations can be utilized; the former is labor intensive in the field, while the latter is most time-consuming post-cruise. In this study, we evaluate the utility of these two methods for a large species in a subpolar environment. This study, together with a concurrent laboratory study of egg production, development and growth rates of *N. flemingeri* (Slater and Hopcroft, in review), provides a fuller understanding of the role of *N. flemingeri/plumchrus* in the ecosystem of the northern Gulf of Alaska.

## METHOD

The study area in the northern Gulf of Alaska has been sampled as part of the U.S. Northeast Pacific GLOBEC program (Weingartner *et al.*, 2002). The region is characterized by a shelf of 100- to 300-m depth, with complex bathymetry and many deep-water coastal fjords and embayments (Fig. 1.1). In each of 2001, 2002, and 2003, six cruises were conducted in March, April, May, June/July, August, and October, while in 2004 the April and August cruises were not undertaken. In 2005, only a single cruise occurred in May. Experimental work was carried out at four stations along the Seward line from inshore to just past the shelf break (i.e. GAK1, 4, 9, 13), plus one station in the western inner passage of Prince William Sound (PWS-either KIP2 or nearby PWS2) where the depth is 500–800 m (Fig. 1.1). Water samples for assessment of ambient phytoplankton concentration at these stations were collected at multiple depths with 5-L Niskin bottles on a CTD rosette, serially size fractionated using 20- $\mu$ m Poretics, 5- $\mu$ m Nuclepore and GF/F filters, with frozen samples later analyzed fluorometrically using techniques for chlorophyll *a* (Chl *a*) (Stockwell and Whitledge, unpublished data).

Seawater for incubations at each station was collected by replicate CTD casts with a 12-place rosette of 10-L Niskin bottles equipped with 9-mm valves to facilitate draining. Collections were typically made within the upper mixed layer, usually from 5- to 20-m depth, but at inshore (GAK 1) and PWS stations, the depths for seawater collection were occasionally greater to avoid salinities of <30 caused by melting snow and glaciers. Incubation seawater was prescreened through 100- $\mu$ m Nitex placed over the ends of Tygon tubing while siphoning the bottles into 20-L soft-walled carboys. Once filled, carboys were stored in a large insulated fish tub (~1 m<sup>3</sup> capacity) rigged as flow-through incubators. The insulated lids of the incubators were fitted with numerous 8-cm plexiglass windows, and the lighting was reduced to ~20% of ambient surface illumination. Food concentrations of incubation seawater at the beginning and the end of experiments were measured as size-fractionated Chl *a* using the same protocols and fluorometric techniques employed for monitoring activities.

At each of the experimental stations, copepods were collected using a 64- $\mu\text{m}$  plankton net with 4-L cod-end hauled slowly from the surface to 50 m and back to the surface ( $\sim 20 \text{ m}^3$  of water filtered) between 08:00 and 12:00 hours. Immediately upon retrieval, copepod collections were diluted using the prescreened seawater and placed into an incubator at ambient surface-water temperatures. Soon after, copepods were sorted into ‘artificial cohorts’ (Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Hopcroft and Roff, 1998; Hopcroft *et al.*, 1998) by sequential passage through submerged screens of the following mesh sizes: 1800, 1300, 1000, 800, 600, 500, 400, 300, 200, 150 and 100  $\mu\text{m}$ . The sample was constantly diluted with prescreened water at ambient seawater temperature, and as each cohort size class was created, it was placed into an incubator at ambient seawater temperature. Under ideal conditions, creating the cohort took 1 hour, but required as much as 3 hours when chains of large filamentous algae were abundant.

Prior to incubation, each size fraction was gently homogenized and evenly divided. One-half was concentrated and preserved in 5% buffered seawater formalin as the time zero sample (T-0) and the other half equally divided among several of the 20-L carboys previously filled with prescreened seawater. The number of carboys employed varied depending on the biomass of copepods being added. The labeled carboys were put back into the on-deck incubators and maintained at surface-water temperatures by running seawater. The temperature inside the incubators was recorded by Onset Tidbit loggers. Ship movement provided constant jostling and ‘mixing’ of the carboys. After 5 days, the carboys were screened through 45- $\mu\text{m}$  mesh, copepods pooled by the original size fractions and preserved immediately in 5% buffered seawater formalin as the final sample (T-5). All preserved material was stained with Rose Bengal.

Concurrent experiments were carried out for *N. flemingeri/plumchrus* at the same stations by picking active and undamaged stage C1–C4 copepodites from additional 64- $\mu\text{m}$  plankton net collections. At least 60, and up to 300, of each stage present were picked and incubated under the identical conditions as the artificial-cohort experiments. Ideally, the two species would have been separated for experimentation, but this proved impractical at sea for these early stages. Nonetheless, our impression is that samples were

predominantly *N. flemingeri*, particularly for the earlier months and more inshore stations. For C5 copepodites, we were unable to observe molting or growth due to the long duration of lipid accumulation prior to diapause. To explore the effect of food enhancement on growth rate, additional single-stage experiments were carried out onboard in March and April of 2003 to which *Isochrysis* sp. (cell length 5–6  $\mu\text{m}$ ) and *Pavlova lutheri* (cell length 6–10  $\mu\text{m}$ ) were added.

In the laboratory, preserved copepods were identified and staged (Miller, 1988; Kobari and Ikeda, 2001), prosome lengths were digitally measured (Roff and Hopcroft, 1986), and the progression of the cohorts was determined by changes in the stage and body size. Separation of early copepodites of *N. flemingeri* and *N. plumchrus* also proved problematic in the laboratory, so the two species were grouped. Development time was calculated as  $1/MR$ , where  $MR$  is the observed molt rate. Weights were predicted based on a prosome length ( $PL$ ) to dry weight ( $DW$ ) relationship:

$\log_{10}[DW] = 3.56 \times \log_{10}[PL] - 2.32$ , where  $PL$  is in mm and  $DW$  is in mg (Slater and Hopcroft, in review). The instantaneous weight-specific growth rates ( $\text{day}^{-1}$ ) within a given cohort, over the incubation time  $t$  (days), were computed from the equation  $g = (\ln W_t - \ln W_0) t^{-1}$  (Runge and Roff, 2000). Recent concerns over growth rate errors using the molt rate method (Hirst *et al.*, 2005) do not apply in this study, because we employed incubation periods not development time to estimate our growth rates.

The relative effects of initial copepodite stages, incubation temperatures and total Chl *a* concentrations on the growth rates were estimated by backward stepwise-regression analysis (SAS system V8). We explored the explanatory power of Chl *a* measured both within our experiments and in the upper 30m at the time of collection. We also explored the effect of  $\log_{10}$  transformation on growth rate and Chl *a* concentration, as this has been shown to linearize such data (Hirst and Bunker, 2003). For other analyses, we used the regression features within Sigmaplot (V8). When necessary, rates were standardized to 5°C using a  $Q_{10}$  of 2.70 for food-saturated broadcast-spawning copepods (Hirst and Bunker, 2003), which agrees with a previous estimate of 2.78 (Kleppel *et al.*, 1996). To

convert dry weight to carbon content ( $\mu\text{g}$ ), we used a conversion factor of 0.44, the arithmetic mean of carbon content for *N. flemingeri* in the Gulf of Alaska (Miller, 1993).

## RESULTS

### Temperature and food resource

*Neocalanus flemingeri/plumchrus* stage C1–C4 copepodites were only present during March–May cruises. The onboard incubation temperatures were generally 5–6°C, similar to the *in situ* temperatures within the upper mixed layer. The notably higher temperatures in May of 2003 were due to a combination of a warmer year and the relatively late timing of that cruise (i.e. late May vs. early May) (Fig. 1.2).

Average Chl *a* concentrations within the upper 30 m in the study area reflected the progression of the spring bloom. Generally, the lowest Chl *a* concentrations occurred in March, increased in April and peaked in May. Spatially, the highest Chl *a* occurred in PWS during April, in advance of the stations along the Seward Line (Fig. 1.2). The seasonal Chl *a* concentrations (mean  $\pm$  SD) over four consecutive years across all sampling stations were  $0.46 \pm 0.19$  in March,  $2.45 \pm 3.71$  in April and  $2.46 \pm 2.02$  May. The spatial distribution of Chl *a* concentrations in this study area over 4 years typically declined offshore, with corresponding values (mean  $\pm$  SD) of  $3.12 \pm 4.04$  at PWS,  $1.51 \pm 1.63$  at GAK1,  $1.77 \pm 2.56$  at GAK4,  $1.20 \pm 1.34$  at GAK9, and  $1.05 \pm 1.36$  at GAK13. The monthly partitioning of size-fractionated Chl *a* concentration within the prescreened seawater during the sampling seasons was variable (data not shown). Generally, the larger particle Chl *a* ( $>20 \mu\text{m}$ ) averaged 44.5% of the total, the 5- to  $20\text{-}\mu\text{m}$  fraction 27.8% and the remainder ( $\sim 0.5\text{--}5 \mu\text{m}$ ) 27.7%.

### Developmental time and growth rate

The development and growth of *N. flemingeri/plumchrus* C1–C4 copepodites estimated during five consecutive years by the artificial-cohort and single-stage methods showed similar patterns, although the artificial-cohort method appeared to produce more variable results (Fig. 1.3).

The single-stage method showed the most consistent patterns; only the first two copepodite stages were common in March, the first four copepodite stages were present in April, and only copepodite stages C3 and C4 (plus the non-incubated stage C5) were common in May. In March, the stage durations were >30 days, and growth rates were slow ( $\sim 0.05 \text{ day}^{-1}$ ), with the exception of PWS where growth and development were much faster, and late March 2004 which is more consistent with April observations. In April, the first three copepodite stages shared comparable stage durations of  $\sim 10$  days, with growth rates ranging from  $0.10$  to  $0.15 \text{ day}^{-1}$ , but spent  $\sim 30$  days at C4, with a relatively low growth rate of  $0.04 \text{ day}^{-1}$ . Overall, growth rates in April appeared to slow down with increasing stage. Similarly, the growth rates declined from C3 to C4 in May, with the C3 growth rate  $\sim 0.16 \text{ day}^{-1}$  and C4 rate of  $\sim 0.10 \text{ day}^{-1}$ , both higher than those observed in April. These patterns become somewhat clearer when averaged by month across years (Fig. 1.4): within each month, stage duration increases with stage and growth rate declines with stage; rates in March are notably slower than other months, while rates in April and May are more similar. Overall growth rates for the first four copepodite stages ranged from  $0.01$  to  $0.22$ , with mean  $\pm$  SE of  $0.11 \pm 0.01 \text{ day}^{-1}$ .

The artificial-cohort method produced more variable results, but the pattern was still comparable and consistent with the single-stage method (Fig. 1.3). In March, only early copepodites of *N. flemingeri/plumchrus* occurred (in mesh sizes ranging from  $400$  to  $800 \mu\text{m}$ ). In April, C1–C4 stages occurred (in mesh sizes from  $400$  to  $1300 \mu\text{m}$ ). In May, early copepodites were virtually absent (and the mesh sizes ranged from  $600$  to  $1800 \mu\text{m}$ ). In March, the mean stage durations were  $\sim 20$ – $35$  days and mean growth rates  $\sim 0.05$ – $0.07 \text{ day}^{-1}$ . During April, copepodites experienced high growth ( $\sim 0.13 \text{ day}^{-1}$ ) and short stage duration ( $< 15$  days) with decreasing growth as the animals became larger and older. In May, growth rates remained high, but not significantly different from those in April, with a trend of decreasing growth with increased stage (Fig. 1.4). Overall, growth rates for the first four copepodite stages by artificial-cohort method were from  $0.01$  to  $0.28$ , with mean  $\pm$  SE of  $0.11 \pm 0.01 \text{ day}^{-1}$ .

### Food enhancement experiment

Food addition resulted in a modest enhancement of the growth rate for *N. flemingeri/plumchrus* (Fig. 1.5); the increases were significant (two-tail paired *t*-test,  $P < 0.001$ ; Wilcoxon signed-rank test,  $\alpha = 0.001$ ). The average growth rate for C1 was increased about 16% by a 25-fold increase in Chl *a* (to  $4.89 \text{ mg m}^{-3}$ ), for C2 an increase of ~15% by a 20-fold increase of Chl *a* (to  $4.27 \text{ mg m}^{-3}$ ) and for C3 an increase of ~8% by 10-fold increase of food concentration (to  $3.25 \text{ mg m}^{-3}$ ). There was only one paired experiment for C4, with a 28% increased growth rate from a 52-fold increase of Chl *a* (to  $4.17 \text{ mg m}^{-3}$ ). In general, copepods in food-enhanced experiments looked healthier than those without food addition.

### Body size and growth rate

Consistent with the relationships between growth rate and stage, growth rate on average declined with increased body size (Fig. 1.6, Table 1.1). Simultaneously, the variability in growth rate declined with body size using both methods. Interestingly, when examined on a per stage basis, for both C1 and C2, there was a positive relationship (Table 1.1,  $r^2 = 0.19\text{--}0.76$ ) between growth rate and body size, regardless of the method. The relationships were also positive for C3 and C4 by the single-stage method (Fig. 1.6; Table 1.1), while patterns were somewhat contradictory for the artificial-cohort methods. The poorer relationship by the artificial-cohort method arises because multiple stages exist in most initials; yet, we force this fractional average initial stage to the nearest whole-numbered stage in this analysis, thus blurring the underlying patterns. Not surprisingly, combining the two methods generally resulted in a reduction of the variability explained, because weights at initial stage were not perfectly comparable between the methods. The existence of these positive relationships within a stage indicates that when growth rate is fastest, individuals within the stage tend to be larger.



### Statistical analysis of growth rate

Developmental stage, temperature and Chl *a* were significant explanatory variables for the single-stage method ( $r^2=0.26$ ,  $P<0.0001$ ), while for the artificial-cohort method ( $r^2=0.13$ ,  $P=0.0011$ ) only stage and Chl *a* were significant (Table 1.2). Combining both types of experiments resulted in slightly poorer fit ( $r^2=0.17$ ,  $P<0.0001$ ). Untransformed data showed the same patterns and explained a similar degree of variation.

After removing the influence of temperature through  $Q_{10}$  standardization, *N. flemingeri/plumchrus* copepodite growth rates estimated by both the artificial-cohort and the single-stage methods showed significant Michaelis–Menten relationships to Chl *a* concentration (Fig. 1.7). Although we had begun this fitting exercise by stage, because we had shown it to be a significant variable in the previous analysis, curves for C1–C3 were very similar with high  $r^2$ , so we combined those stages. For the C1–3 group by both methods, 32–34% of variance in growth rate was significantly explainable by Chl *a* ( $P<0.0001$ ), with the maximum growth rates ( $G_{\max}$ ) of 0.17–0.18 day<sup>-1</sup> and half saturation Chl *a* concentrations ( $K_{\text{chl}}$ ) of 0.45–0.46 mg m<sup>-3</sup>. At C4, Chl *a* accounted for 19% of variance in growth rate using the artificial-cohort method and 30% of variance in growth rate using the single-stage method, with  $G_{\max}$  dropping to 0.08 day<sup>-1</sup> and  $K_{\text{chl}}$  remaining at 0.38–0.66 mg m<sup>-3</sup>. It is notable that both methodologies effectively predict the same underlying relationships to ambient Chl *a* concentration.

## DISCUSSION

This study provides the first comprehensive estimates of *in situ* developmental time and somatic growth rates for *N. flemingeri/plumchrus*. Overall, these rates are comparable with previous estimates. It is notable that the two methods employed in this study are comparable and reveal the same underlying patterns in growth and development rates.

### Developmental time

Development times are in reasonable agreement with the few estimates for this and sibling species determined by incubation or through following natural cohorts in the field

(Table 1.3). On the basis of this study, the developmental time of *N. flemingeri/plumchrus* from the start of C1 to C5 averages ~56 days. This is identical to a 56-day estimate for *N. plumchrus* in the Alaska gyre (Miller, 1993). Under ideal conditions, average development times for C1–C3 are ~10 days each and for C4 ~10–14 days for a total of 40–45 days, which is more comparable with the 46-day estimate in the southern Bering Sea (Vidal and Smith, 1986) and <45 days in Oyashio region (Tsuda *et al.*, 1999). It is notable that the only previous direct measurements of development rate (i.e. by incubation) for any *Neocalanus* spp. were the 21.3-day estimate for C4 *N. plumchrus* (Miller and Nielsen, 1988). All these estimates suggest that the recent indirect estimates of development time at colder temperatures deduced using *Calanus* spp. as an analogue (Saito and Tsuda, 2000) may be too fast.

In this region, the entire developmental time of *N. flemingeri/plumchrus* from egg hatching to C5 is 119–123 days, estimated by adding the stage durations of copepodite at C1–C4 from this study with the laboratory-estimated 63–67 days for naupliar stages at 5°C (Slater and Hopcroft, in review) assuming that laboratory measurements reflect the field values. Again, this value is in reasonable agreement with other estimates, e.g. 4 months in the western subarctic Pacific (Tsuda *et al.*, 1999) and 3.5–4 months in the central Gulf of Alaska (Miller and Clemons, 1988). Despite some minor differences in water temperature, life-cycle timing is very similar between these three regions, with stage C1 appearing in late February to early March and stage C5 predominating by May.

### **Growth rate**

Growth rates of *N. flemingeri/plumchrus* in this study are comparable with other *Neocalanus* spp. in the region (Table 1.3). A comparison of available *in situ* and incubation estimated growth rates of *Neocalanus* spp. in the subarctic Pacific reveals an overall trend of decreasing growth with increasing developmental stages (Table 1.3). This pattern for copepodite stages at C1–C4 compares well with our data ranging from 0.072 to 0.12 day<sup>-1</sup> in this study and the growth rates of 0.11–0.14 day<sup>-1</sup> for *N. plumchrus* in the southeastern Bering Sea (Vidal and Smith, 1986), although our average stage-specific

rates for *N. flemingeri/plumchrus* are slower. The *in situ* growth rates at Station P in the Alaska gyre for *N. plumchrus* at C4 were 0.05 (Miller and Nielsen, 1988), consistent with our field-estimated growth rate of 0.072 day<sup>-1</sup> for that stage of *N. flemingeri/plumchrus*. The growth rate of C5 may increase to 0.10–0.15 day<sup>-1</sup> (Miller and Nielsen, 1988) or continue to decline (Vidal and Smith, 1986); hence it remains unclear what the growth rate of this stage may be. It is notable that the only previous direct measurements of growth rate (i.e. by incubation) for any *Neocalanus* spp. were those for C5 obtained by measuring weight increase within that stage (Miller and Nielsen, 1988). We were unable to estimate growth of this lipid-accumulating stage by our techniques due to its long stage duration.

### **Environmental variables and growth rate**

Food and temperature are the important environmental variables for copepod growth (Mauchline, 1998; Hirst and Bunker, 2003). In aquatic ecosystems, Chl *a* has long been considered as a general index of food concentration, although for some species it may be a poor predictor of growth and fecundity (Hirst and Bunker, 2003; Bunker and Hirst, 2004). In this study, total Chl *a* appears to be a reasonable food index for *N. flemingeri/plumchrus*, as indicated by its relationship to growth rate. *Neocalanus* spp. have been shown to act primarily as suspension feeders on micro-sized (>20 µm) particles but are capable of utilizing food down to 5 µm (Gifford, 1993; Kobari *et al.*, 2003; Liu *et al.*, 2005; Dagg *et al.*, submitted for publication). At times when microzooplankton predominates, this component may form a larger proportion of the diet than phytoplankton (Gifford, 1993; Kobari *et al.* 2003), and this no doubt contributes to some of the scatter in our growth relationships with chlorophyll.

Growth of adult and juvenile copepods can often be food limited (Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Hopcroft and Roff, 1998). Food limitation appears to become more severe with increasing temperature (Hirst and Lampitt, 1998; Richardson and Verheye, 1998); thus food-limitation is pervasive in warm waters and less common in cold waters. Globally, food limitation can affect adult growth more

substantially than juvenile growth (Hirst and Bunker, 2003). In this study, the growth of *N. flemingeri/plumchrus* also appeared to be food limited. The predicted food saturation ( $G_{\max}$ ) growth rate for C1–C3 was 0.17–0.18 day<sup>-1</sup>. While some rates exceeded these, many field values were below this saturated rate in March (prior to significant increase in phytoplankton biomass) and for later stages in May when the chlorophyll bloom remained variable in its timing. Food limitation is also suggested by our experimental addition of food, although the impact was relatively limited over the 5-day duration employed in this study. Interestingly, although food addition resulted in elevated growth rates, values remained well below  $G_{\max}$ , although the Chl *a* concentrations were much higher than the  $K_m$ . This implies that either there is considerable “inertia” in somatic growth rates within *N. flemingeri/plumchrus* (that requires time for a response to be realized) or the food offered (*Isochrysis* sp. and *Pavlova lutheri*) were too small to be captured efficiently (Richardson and Verheye, 1999). Finally, food-limited growth in the field is also supported by comparing field values with laboratory-determined values (Table 1.3), and it is likely to underlie the variability observed between stations and years in this study.

### **Comparison to global models**

Growth is a key component in understanding the role of copepods in material flow and transformation in the sea; however, estimating *in situ* somatic growth rates is time consuming and effort intensive. In the past decade, attempts have been made to make predictions from a few easily measurable parameters such as temperature (Huntley and Lopez, 1992), temperature and body weight (Hirst and Sheader, 1997; Hirst and Lampitt, 1998) or temperature, body weight and food concentration (Hirst and Bunker, 2003). Predictive global models are necessary to make the estimation of growth, and hence secondary production over large spatial and temporal scales is feasible. There is, therefore, a constant need to test and refine such models by comparing them with new rates, such as those directly measured in this study, and exploring the utility of such models in specific study areas.

The simplest of these global models (Huntley and Lopez, 1992) considers only temperature, which has long been known to influence biological rates. It is clear that this model fails to capture the underlying form of growth rate observed in this study (Fig. 1.8). A more complex model, incorporating both temperature and body size (Hirst and Lampitt, 1998), more adequately reflects the patterns we observed (Fig. 1.8). The most complex models, which incorporate temperature, body size and chlorophyll concentration (Hirst and Bunker, 2003), come closer to our observations (Fig. 1.9), at least for their models of adult broadcasters and all their data combined. Nonetheless, the potential errors associated with these models can be large (Table 1.4). All the predictions by the models of Huntley and Lopez, Hirst and Lampitt, and the two models of Hirst and Bunker (adult broadcasters and all data) noticeably underestimate by 10% up to 60%. In contrast, the model of Hirst and Bunker for juvenile broadcasters seriously overestimates by 3- to 8-fold the observations in this study (Table 1.4).

The lack of predictive power of these equations is not surprising, considering that all these empirical models had few data on species living in cold waters around 5°C, especially for juvenile somatic growth, and almost no data from the sub-arctic Pacific. It is interesting to find that the predictions by the simple temperature-dependent model of Huntley and Lopez (Huntley and Lopez, 1992) are closer to the direct estimates (Table 1.4), in part because their relationship tends to represent maximum temperature-dependent rates. At the same time, this simple model fails to capture the body-size pattern present in our data. The Huntley–Lopez model may be even less satisfactory in oligotrophic waters (Calbet and Agusti, 1999), where it results in overestimation, because growth is seldom maximal due to food limitation.

The more recent models of Hirst and Lampitt (Hirst and Lampitt, 1998) are clearly improvements over the Huntley and Lopez model and have already been employed in a number of studies (Roman *et al.* 2000, 2002; Coyle and Pinchuk, 2003), but to our knowledge have only been tested in a few cases (Richardson *et al.*, 2001, Peterson *et al.*, 2002; Rey-Rassat *et al.*, 2004) where success has been variable. These equations have already been superseded by a more sophisticated effort (Hirst and Bunker, 2003). Both of

these models generally indicate a negative relationship with body size, which agrees with the overall pattern for all data in our study. What is interesting is the positive relationship between growth and body size within a stage shown by our data. Although such a pattern can be demonstrated in the laboratory (Vidal, 1980a, b), it is not normally detectable in the field. Such a pattern arises because when populations are growing rapidly, size at stage is large because the animals have been well fed, while populations that have not been well fed grow slowly and hence are smaller at stage. The loss of clarity in these relationships with increasing stage probably arises because later stages are more likely to have experienced a mixture of favorable and unfavorable growth conditions during their lives, and hence they are more variable in size. These within-stage relationships are simply lost within the high variability present in the data sets used to construct global models; yet, in the case of *Neocalanus*, they are sufficiently strong that they can be used to predict growth from simple knowledge of size at stage.

Clearly, there is still a need to refine these models, particularly in polar and subpolar environments. This requires the continued generation of data on growth rates from a wide variety of species. Initially, the artificial-cohort method was developed to address the difficulty of sorting by stage, continuously reproducing copepod populations of smaller species (Kimmerer and McKinnon, 1987). The application of the artificial-cohort technique, and its modifications, has been successful in warmer waters (Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Hopcroft *et al.*, 1998; Campbell *et al.*, 2001; McKinnon and Duggan, 2003), but this study represents the first validation of the technique in colder waters. Although the technique yields more variability than the single-stage method, it ultimately reveals the same underlying relationships with food resources. The single-stage method, while arguably superior, is only practical for larger species where stages may be more readily separated. Furthermore, a significant attraction of the artificial-cohort method is that it can be routinely performed at sea, whereas the single-stage method requires working conditions suitable for live sorting. Last, the artificial-cohort method provides data simultaneously on all the dominant species present in a collection, while it is difficult to prepare single stages of more than one species

concurrently. Thus, the artificial-cohort method appears to be the most practical method for local estimation of copepod community production, and the refinement of more global models.

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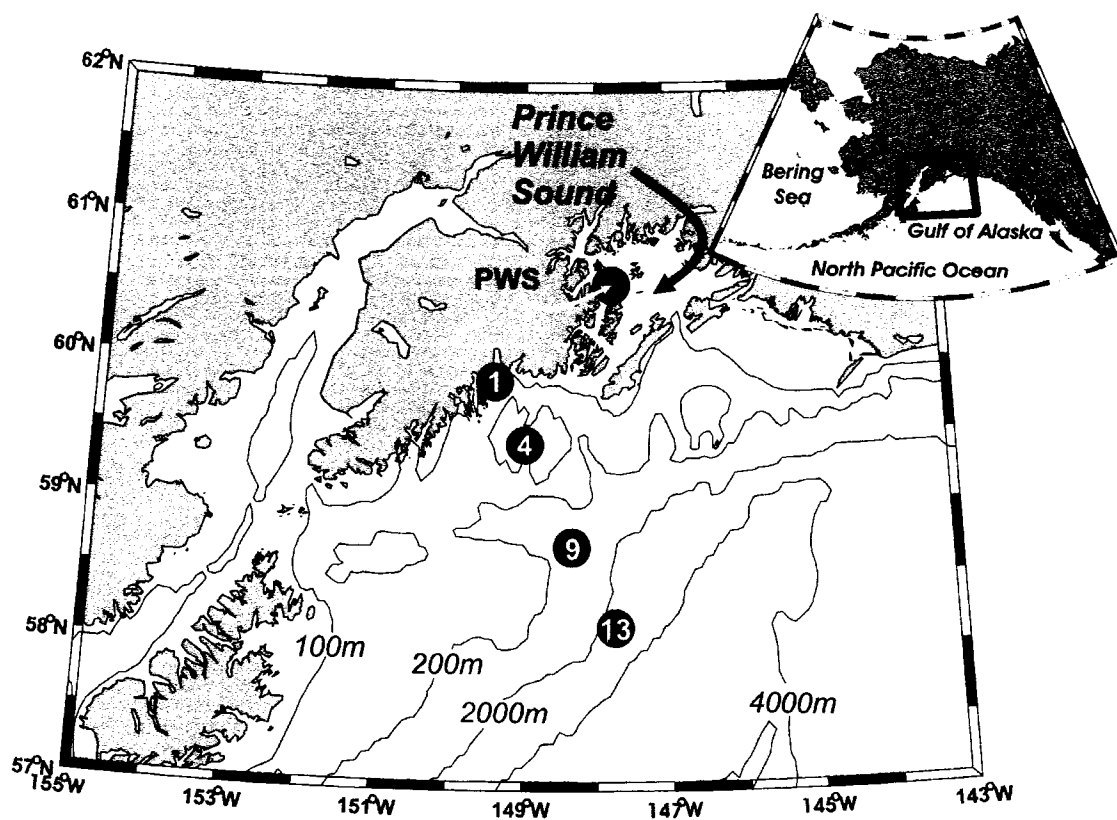
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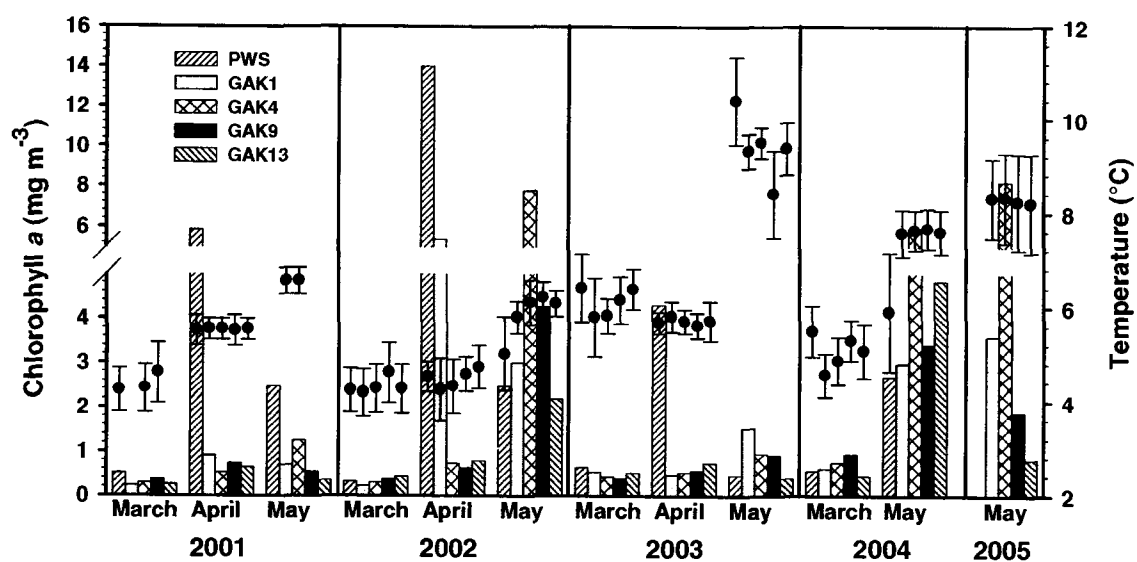
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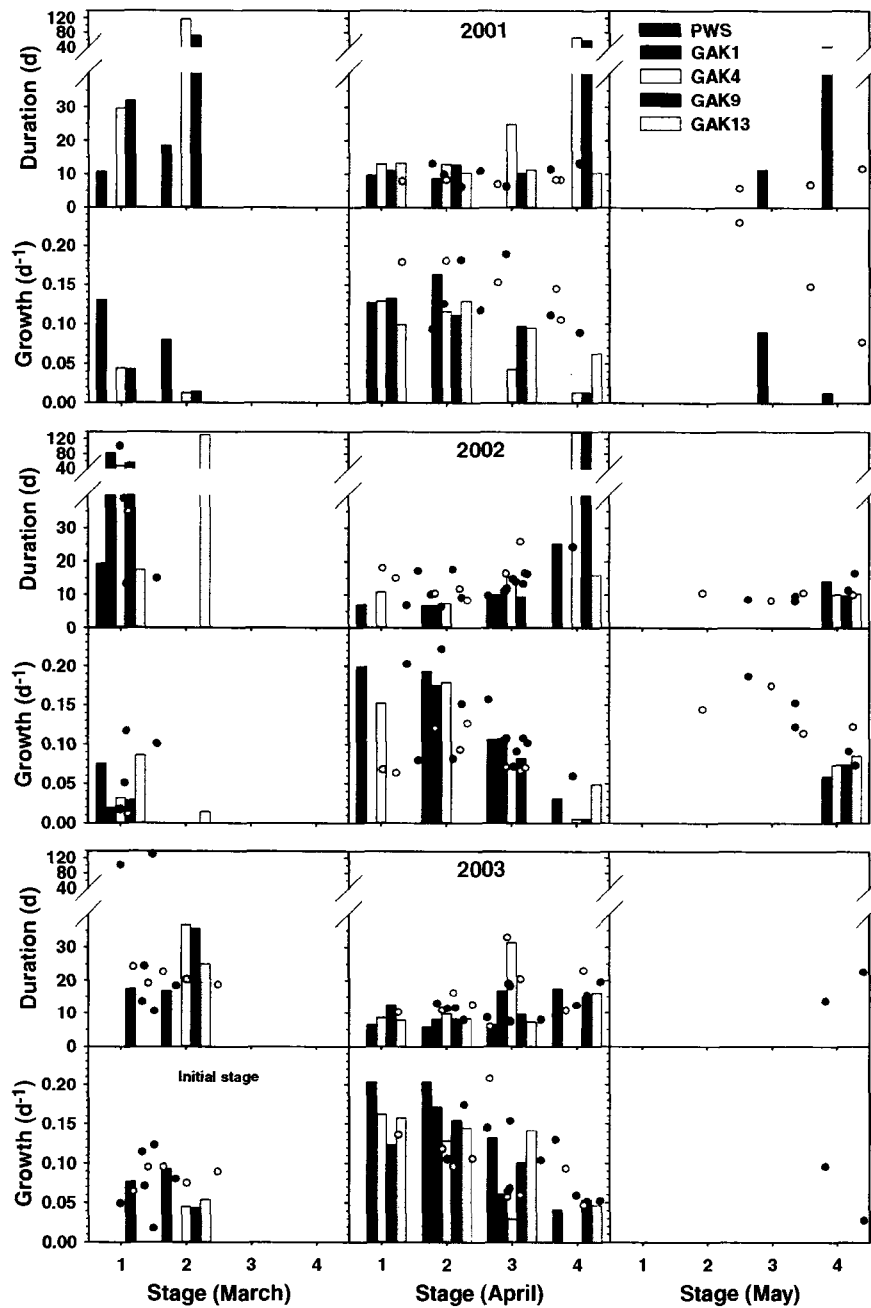
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**Figure 1.1** Map of sampling locations in the northern Gulf of Alaska study region.

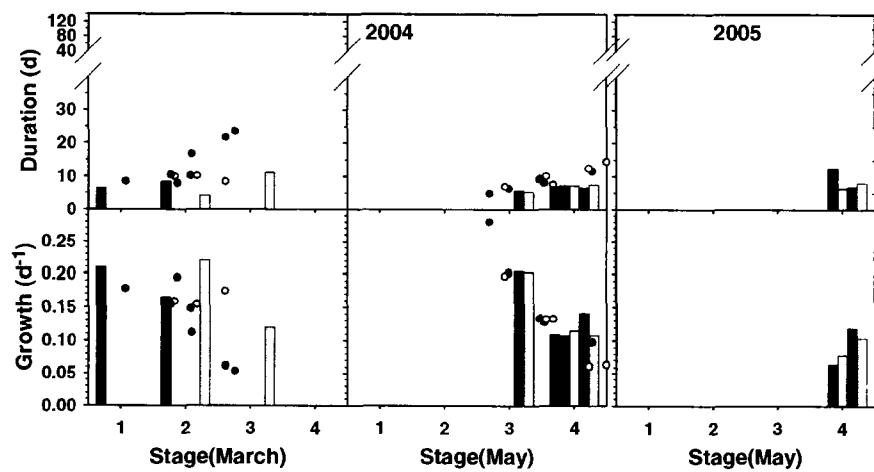


**Figure 1.2** Chlorophyll *a* (Chl *a*) concentration at study sites averaged over the upper 30 m (bars) and incubation temperatures of experiments at sea in the northern Gulf of Alaska 2001–2005 (circles). Error bars are SD.

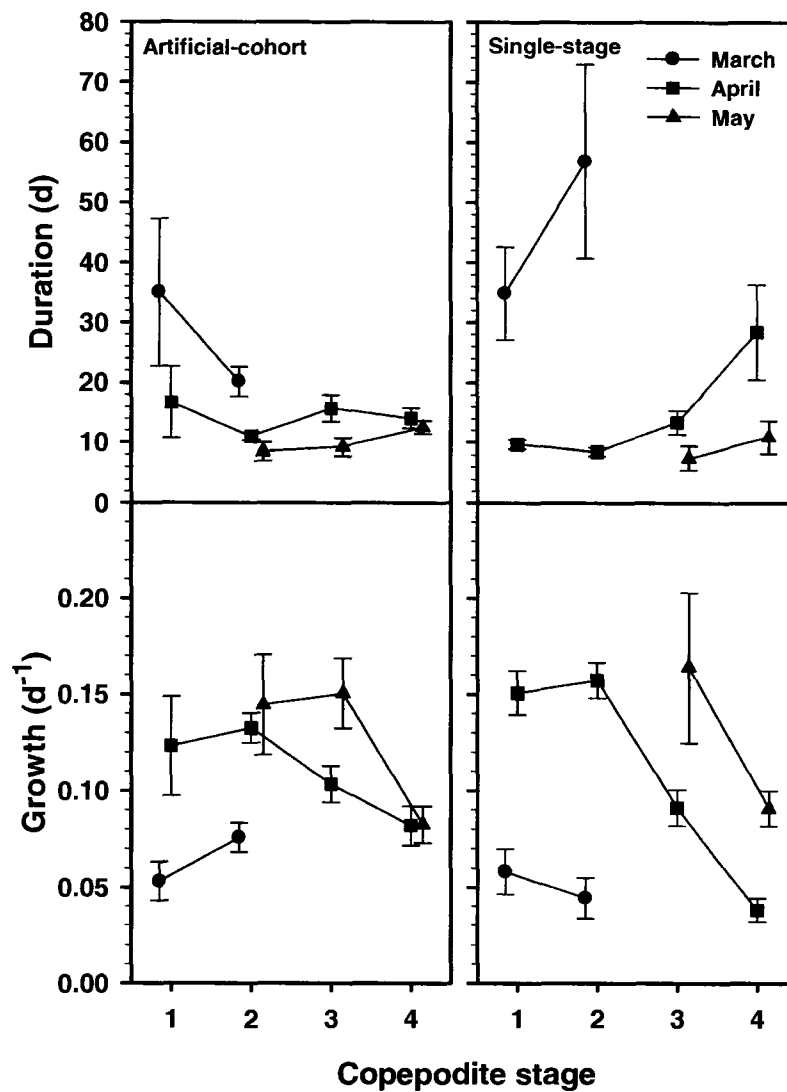


**Figure 1.3** Stage durations (upper panels) and growth rates (lower panels) of *Neocalanus flemingeri/plumchrus* in the northern Gulf of Alaska 2001–2005. For the single-stage method (bars), initial stages are integers, while for the artificial-cohort method (circles) stage is the average of the population at time-zero.

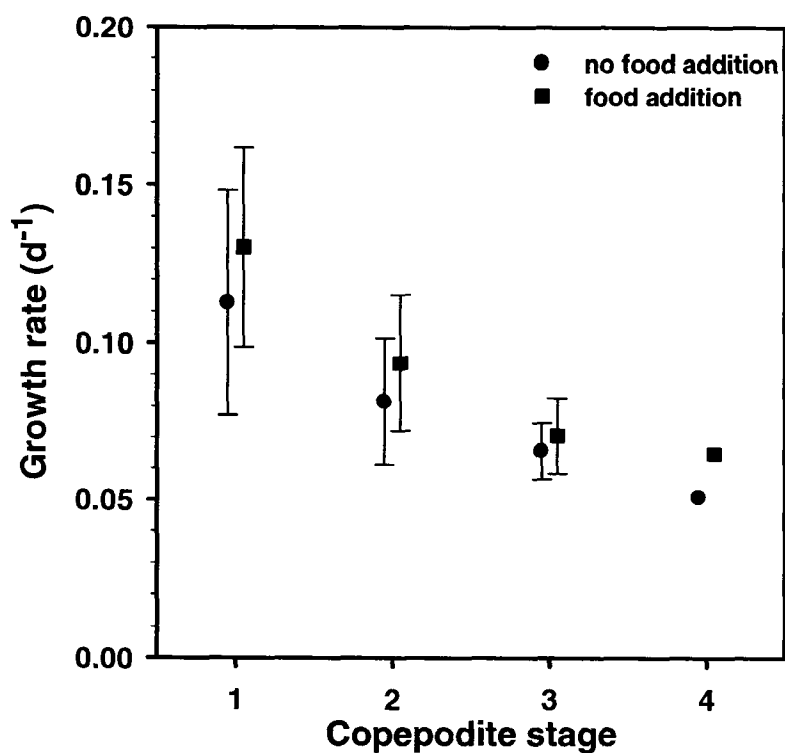




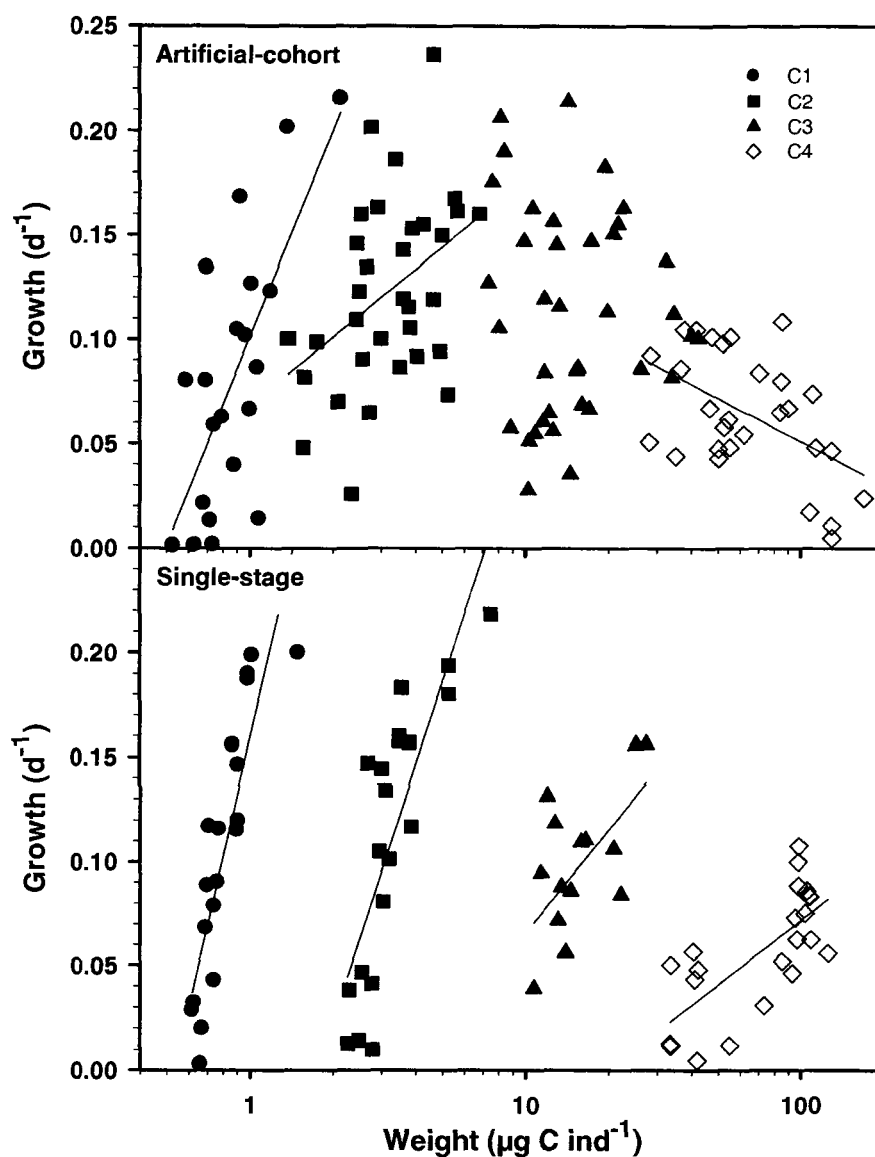
**Figure 1.3** (continued) Stage durations (upper panels) and growth rates (lower panels) of *Neocalanus flemingeri/plumchrus* in the northern Gulf of Alaska 2001–2005. For the single-stage method (bars), initial stages are integers, while for the artificial-cohort method (circles) stage is the average of the population at time-zero.



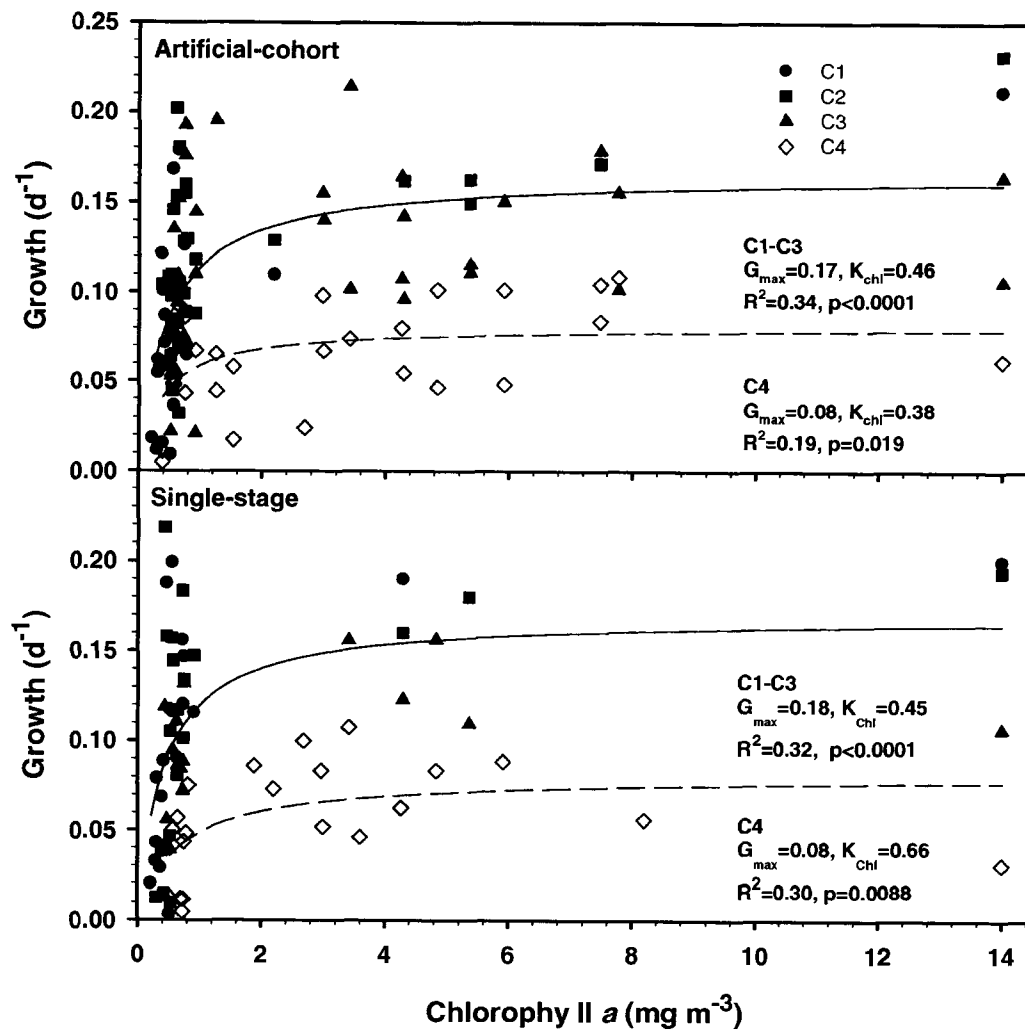
**Figure 1.4** Monthly mean stage duration and growth rate versus *Neocalanus flemingeri/plumchrus* copepodite stage estimated by artificial-cohort and single-stage methods in the northern Gulf of Alaska 2001-2005. Values plotted against initial stage and offset to improve interpretation. Error bars are SE.



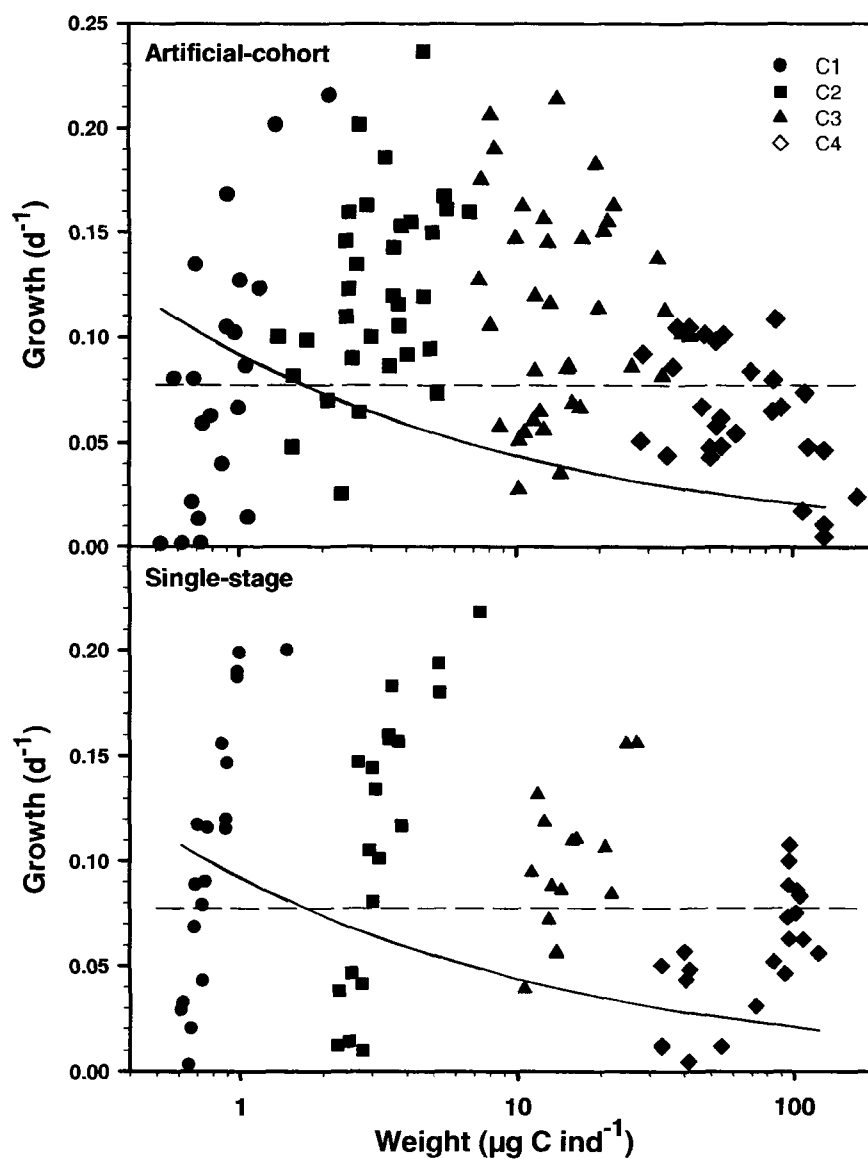
**Figure 1.5** Effect of food enhancement on growth rate of *Neocalanus flemingeri/plumchrus* in the northern Gulf of Alaska. Error bars are SE.



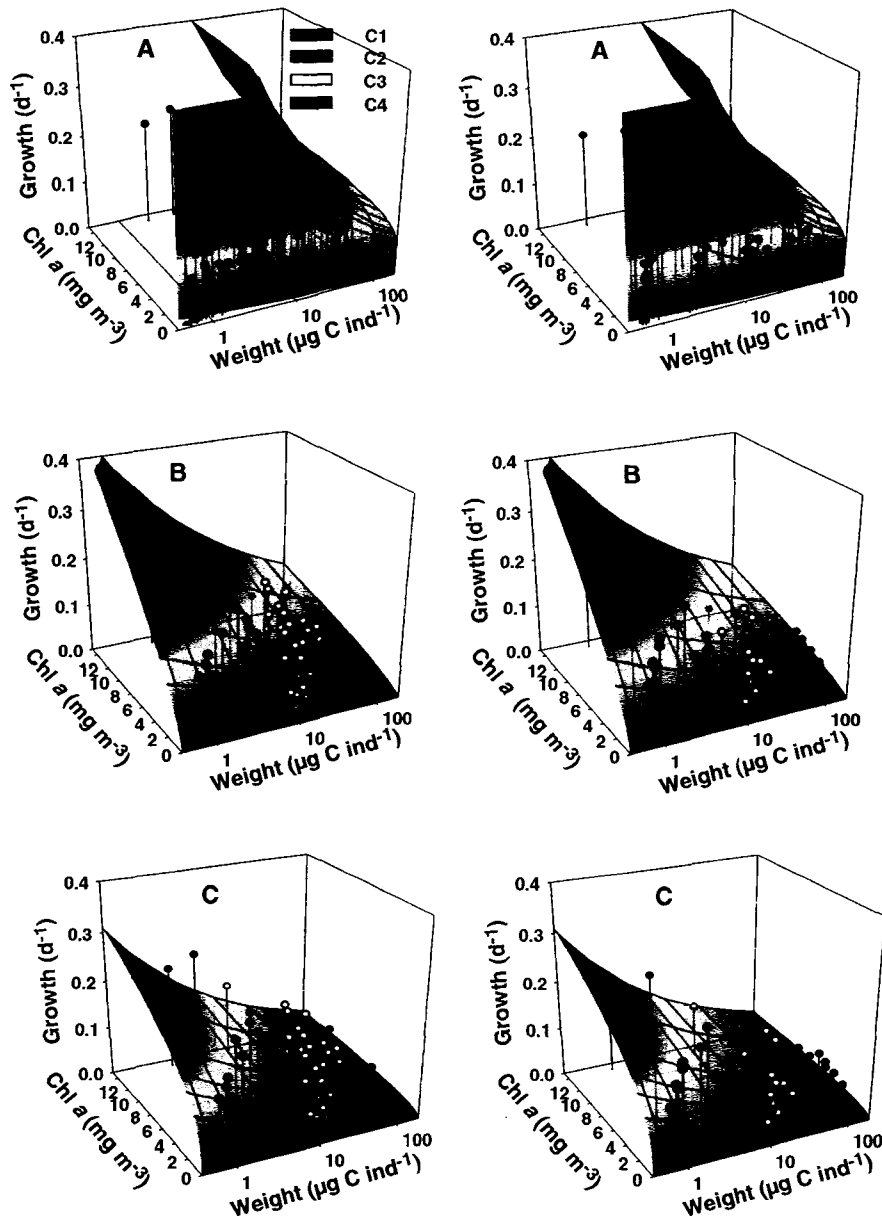
**Figure 1.6** Relationship between growth rate of *Neocalanus flemingeri/plumchrus* and the body weight ( $\mu\text{g C individual}^{-1}$ ) within early copepodite stages estimated by artificial-cohort and single-stage methods in the northern Gulf of Alaska.



**Figure 1.7** Functional relationship between temperature-corrected growth rates estimated by the artificial-cohort and single-stage methods and chlorophyll *a* (Chl *a*) for *Neocalanus flemingeri/plumchrus* in the northern Gulf of Alaska. Michaelis-Menten curves fitted for C1–C3 (solid line), and for C4 (dashed line).



**Figure 1.8** Comparisons of temperature-corrected *Neocalanus flemingeri/plumchrus* growth rates estimated by the artificial-cohort and single-stage methods in this study to those predicted at 5°C by models. Dashed line, Huntley and Lopez (1992); Solid line, Hirst and Lampitt (1998) equation for all data (adults and juveniles of both broadcast and sac-spawners).



**Figure 1.9** Comparisons of temperature-corrected *Neocalanus flemingeri/plumchrus* growth rates in this study with those predicted by the Hirst and Bunker (Hirst and Bunker, 2003) model at 5°C (colored surface). Left column, artificial-cohort method; right column: single-stage method. (A) For juveniles broadcasters; (B) for adult broadcasters; (C) for all data combined.

**Table 1.1** Analysis of growth rate ( $Gr \text{ day}^{-1}$ ) versus body weight ( $BW \mu\text{g C individual}^{-1}$ ) grouped by *Neocalanus flemingeri/plumchrus* copepodite stages for the northern Gulf of Alaska over 4 years

	Copepodite Stage	No. of data	Corrected temperature	$Gr=a+b*\log BW$		$r^2$	$P$
				Intercept (a)	Slope (b)		
Artificial-cohort	C1	21	5	0.101	0.328	0.503	<0.0005
	C2	34	5	0.068	0.108	0.194	0.009
	C3	37	5	0.125	-0.001	0.002	0.806
	C4	28	5	0.189	-0.069	0.252	0.006
	All	111	5	0.104	-0.011	0.022	0.124
Single-Stage	C1	19	5	0.159	0.581	0.76	<0.0001
	C2	20	5	-0.099	0.409	0.66	<0.0001
	C3	15	5	-0.099	0.165	0.37	0.017
	C4	21	5	-0.133	0.102	0.51	0.0002
	All	76	5	0.107	-0.017	0.057	0.038
Combined	C1	40	5	0.121	0.381	0.504	<0.0001
	C2	54	5	0.031	0.174	0.288	<0.0001
	C3	52	5	0.097	0.010	0.002	0.765
	C4	46	5	0.064	-0.002	0.0002	0.923
	All	187	5	0.105	-0.014	0.035	0.010



**Table 1.2** Backward multiple regression analysis of the weight-specific growth rate regressed on the initial stage (*Stg*), incubation temperature (*T* °C) and chlorophyll *a* (Chl *a*) concentration (*Chl* µg l<sup>-1</sup>) of *Neocalanus fleminigeri/plumchrus*

Group	Dependent	n	$\text{Log}_{10}g = a_1Stg + a_2T + a_3\log_{10}Chl + a_4$				$r^2(p)$
			$a_1(p)$	$A_2(p)$	$a_3(p)$	$a_4(p)$	
Artificial-cohort	Stg, T, Chl	111			0.2903 ( $<0.0001$ )	-1.0818 ( $<0.0001$ )	0.1358 ( $<0.0001$ )
Single-stage	Stg, T, Chl	76	-0.1469 (0.0005)	0.0919 (0.0315)	0.3425 (0.0005)	-1.2894 ( $<0.0001$ )	0.2432 (0.0002)
Combined	Stg, T, Chl	187	-0.0820 (0.0049)	0.0440 (0.0910)	0.3388 ( $<0.0001$ )	-1.1468 ( $<0.0001$ )	0.1587 ( $<0.0001$ )

**Table 1.3** Growth rates corrected to 5°C and development times (in parentheses) for *Neocalanus* species in the subarctic Pacific

Species	Temp(°C)	Growth rate and developmental time						Location	Source
		C1	C2	C3	C4	C5	Average		
<i>N. flemingeri/plumchrus</i>	5.0-6.0	0.117 (14.1)	0.122 (13.1)	0.109 (12.4)	0.072 (13.5)		0.105 (13.3)	Gulf of Alaska	This study
<i>N. flemingeri</i>	5.0		0.14 (11)	0.12 (12)	0.07 (15)		0.11 (13)	Gulf of Alaska	Slater and Hopcroft, (in review)
<i>N. flemingeri</i>						0.10		Gulf of Alaska	Miller and Nielsen (1988)
<i>N. plumchrus</i>				(24)	0.05 (21.3 or 25)	0.15		Gulf of Alaska	Miller and Nielsen (1988)
<i>N. plumchrus</i>				(13.4)				Gulf of Alaska	Miller (1993)
<i>N. plumchrus</i>	0.5-6.0	0.143 (8)	0.141 (10)	0.133 (12)	0.111 (16)	0.039 ( )	0.113 (11.5)	Southeastern Bering Sea	Vidal and Smith (1986)
<i>N. cristatus</i>	0.5-6.0		0.075 (17)	0.072 (20)	0.066 (23)	0.045 ( )	0.065 (20)	Southeastern Bering Sea	Vidal and Smith (1986)

**Table 1.4** Comparison of growth rates predicted by the global models at 5°C with *Neocalanus flemingeri/plumchrus* *in situ* growth rates corrected to 5°C

Data source	Percent of predicted to rates of this study				
	C1	C2	C3	C4	C1-C4
Huntley and Lopez (1992)	84%*	66%	71%	117%	79%
Hirst and Lampitt (1998)	106%*	54%	36%	37%	56%
Hirst and Bunker (2003)a	719%	367%	245%	249%	380%
Hirst and Bunker (2003)b	54%	40%	47%	64%	49%
Hirst and Bunker (2003)c	75%	47%	42%	51%	52%

\* non-significant at  $\alpha=0.05$ , two sample t-Test assuming unequal variance.

In Hirst and Bunker (2003), a: for juvenile broadcasters; b: for adult broadcasters; c: for all data.

***Chapter 2*****Growth and development of *Metridia pacifica* (Copepoda: Calanoida) in the northern Gulf of Alaska\***

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**ABSTRACT**

Juvenile growth and development rates for *Metridia pacifica*, one of the dominant larger copepods in the subarctic Pacific, were investigated from March through October of 2001–2004 in the northern Gulf of Alaska. The relationship between prosome length (PL,  $\mu\text{m}$ ) and dry weight (DW,  $\mu\text{g}$ ) was determined:  $\log_{10}DW = 3.29 \times \log_{10}PL - 8.75$ . The stage durations of copepodites ranged from 3 to 52.5 days but were 8–15 days under optimal conditions. Seasonally, growth rates increased from March to October and typically ranged between 0.004 and 0.285  $\text{day}^{-1}$ , averaging  $0.114 \pm 0.007 \text{ day}^{-1}$  (mean  $\pm$  SE). After standardization to 5°C ( $Q_{10}$  of 2.7), growth rates averaged  $0.083 \pm 0.005 \text{ day}^{-1}$  and were significantly correlated to chlorophyll *a*, with saturated growth rates of 0.149  $\text{day}^{-1}$  for C1–C3, 0.102  $\text{day}^{-1}$  for C4–C5 and 0.136  $\text{day}^{-1}$  for all stages combined. Measured juvenile growth rates were comparable to specific egg production rates in this species. The comparisons of our rates in this study with those predicted by the global models of copepod growth rates suggested that further refinement of these models is required.

**Key words:** *Metridia pacifica*, growth, development, artificial-cohort, Gulf of Alaska

## INTRODUCTION

Copepods are the major component of mesozooplankton throughout the world's oceans (Verity and Smetacek, 1996) and play an important role in the marine ecosystem linking primary production to upper trophic levels, accounting for up to 80% of the metazoan biomass in the marine environment (Kiørboe, 1997). Over the past few decades, copepod productivity has become a central aspect of marine plankton research (Runge and Roff, 2000). However, without accurate information on copepod rate processes, our understanding of the trophodynamics of the marine ecosystem will remain incomplete (Longhurst, 1984). Growth is one of the key components required to assess the role of copepods in the matter and energy flows in the sea, yet the *in situ* estimation of somatic growth rates is seldom undertaken because it is time consuming and labor intensive.

At present, we know relatively little about the growth rates of juvenile copepods in nature, with the majority of such work having been done in temperate waters (10–20°C). Increasingly, the egg production approach has been adopted for estimating the growth rate and secondary production of copepods (Poulet *et al.*, 1995; Runge and Roff, 2000), yet the equivalence of egg production and somatic growth rate has been frequently challenged (Hopcroft and Roff, 1998; Richardson and Verheye, 1998; Hirst and McKinnon, 2001; Hirst *et al.*, 2005). Although there is abundant information on egg production rates in cold waters, very little somatic rate work has been done (Hirst and Bunker, 2003) because of the relatively long incubation times required.

*Metridia* species are ubiquitous throughout the world's oceans, occurring from temperate to subpolar waters (Brodsky, 1967), typically undergoing strong diel vertical migration (Hattori, 1989; Batchelder, 1985). In the subarctic Pacific, *Metridia pacifica* is the most common species, is broadly distributed and is among the major components of the zooplankton seasonal cycle (Batchelder, 1985; Vidal and Smith, 1986; Coyle *et al.*, 1990; Incze *et al.*, 1997; Cooney *et al.*, 2001; Coyle and Pinchuk, 2003, 2005; Padmavati *et al.*, 2004). Among the larger-bodied copepods, they are second in abundance only to *Neocalanus* species in spring and early summer, and often rank first during the fall-winter season after the departure of *Neocalanus* species and *Eucalanus bungii* from the upper

mixed layer (Batchelder, 1985; Vidal and Smith, 1986; Coyle and Pinchuk, 2003, 2005; Padmavati *et al.*, 2004). Hence, *Metridia* is ecologically important in the subarctic Pacific during the fall-winter season (Batchelder, 1986; Padmavati *et al.*, 2004) and exerts significant pressure on the phytoplankton during this time (Batchelder, 1986). Several higher trophic levels rely on *Metridia* species as a major component of their diet, such as herring, walleye Pollock and salmon (Brodeur, 1998; Foy and Norcross, 1999; Moku *et al.*, 2000; Armstrong *et al.*, 2005).

Hitherto, several studies of life cycles and grazing impact have been done on *Metridia* species in the north Pacific (Shebanova, 1977; Batchelder, 1985, 1986; Hirawaka, 1991; Hirawaka and Imamura, 1993; Ikeda *et al.*, 2002; Padmavati *et al.*, 2004). Despite their prominence, our knowledge on measured vital rates of *Metridia* are still limited to early development (Pinchuk and Paul, 1998), the mean growth rate from C1 to C5 for *M. pacifica* (Vidal and Smith, 1986), laboratory development times (Padmavati and Ikeda, 2002) and recent data on egg production (Halsband-Lenk, 2005; Hopcroft *et al.*, 2005). Detailed data on juvenile growth of *M. pacifica*, and its functional relationship with other factors such as temperature, chlorophyll *a* (Chl *a*) and body weight, are still missing.

The traditional approach to estimate the *in situ* rates of copepod growth and development involves tracking of natural cohorts by frequent sampling. Realistically, this can only be applied to coastal species, and for oceanic species, the requirement of frequent sampling of a discrete population can seldom be met, particularly in the northern Gulf of Alaska because of its highly advective nature (Weingartner *et al.*, 2002; Stabeno *et al.*, 2004). We employed the “artificial-cohort” method (Kimmerer and McKinnon, 1987) to overcome this obstacle, using techniques recently validated for *Neocalanus* (Liu and Hopcroft, 2006). Here, we present seasonal juvenile growth rates and developmental time of *M. pacifica* in the northern Gulf of Alaska. We explore the functional relationships between growth and food availability, temperature and body size, compare estimated *in situ* somatic growth rate with predicted values by published models and finally develop an empirical predictive model.

## METHOD

Samples were collected and experiments conducted during the U.S. GLOBEC Northeast Pacific Long-Term Observation Program (LTOP) (Weingartner *et al.*, 2002). The study region is characterized by a shelf of 100–300 m depth, with complex bathymetry and many deep-water coastal fjords and embayments (Fig. 2.1). In 2001, 2002 and 2003, six cruises were conducted in March, April, May, June/July, August, and October. Three more cruises occurred in March, May and June/July of 2004. Experimental work was carried out at four stations along the Seward line from inshore to just past the shelf break (i.e. GAK1, 4, 9, 13) and one station along the western inner passage of Prince William Sound (PWS—either KIP2 or PWS2) where the depth is 500–800 m (Fig. 2.1). Water samples for the assessment of ambient phytoplankton concentration at these stations were collected at multiple depths by 5-L Niskin bottles on a CTD rosette, serially size-fractionated using 20  $\mu\text{m}$  Poretics, 5  $\mu\text{m}$  Nuclepore and GF/F filters, with frozen samples later analyzed fluorometrically for Chl *a* concentration (D. A. Stockwell and T. E. Whitley, unpublished data).

Experimental methodology is identical to that previously employed successfully for *Neocalanus* species (Liu and Hopcroft, 2006). Seawater for incubations at each station was collected by replicate CTD casts with a 12-place rosette of 10-L Niskin bottles equipped with 9-mm valves. Collections were typically made within the upper mixed layer, usually from 5 to 20 m depth, but at inshore (GAK1) and PWS stations, the depths for collection were occasionally deepened to avoid salinities <30 caused by melting snow and glaciers. Incubation seawater was pre-screened through 100- $\mu\text{m}$  Nitex mesh sacs placed over the ends of Tygon tubing while siphoning the bottles into 20-L soft-walled carboys. Once filled, carboys were stored in large insulated fish tubs ( $\sim 1 \text{ m}^3$  capacity) rigged as flow-through incubators. The insulated lids of the incubators were fitted with numerous 8-cm plexiglass windows and reduced lighting to  $\sim 20\%$  of ambient surface illumination. Food concentrations of incubation seawater at the beginning and the end of experiments were measured as size-fractionated Chl *a* using the same protocols and fluorometric techniques employed for monitoring activities.



At each of the experimental stations, copepods were collected using a 64- $\mu\text{m}$  plankton net with 4-L cod-end fished slowly from the surface to 50 m and back to the surface ( $\sim 20 \text{ m}^3$  of water) between 0800 and 1200 h. Immediately on retrieval, copepod collections were diluted using the pre-screened seawater and placed into an incubator at ambient surface water temperatures. Soon after, copepods were sorted into “artificial cohorts” (Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Hopcroft and Roff, 1998; Hopcroft *et al.*, 1998) by sequential passage through submerged screens of the following mesh sizes: 1800, 1300, 1000, 800, 600, 500, 400, 300, 200, 150 and 100  $\mu\text{m}$ . The sample was constantly diluted with pre-screened water cooled at ambient seawater temperature, and as each cohort size class was created, it was placed into an incubator at ambient seawater temperature. Under ideal conditions, this cohort-creating process took 1 hr and as much as 3 h when chains of large filamentous algae were abundant.

Before incubation, each size fraction was gently homogenized and evenly divided. One-half was concentrated and preserved in 5% buffered seawater formalin as the time zero sample (T-0), and the other half equally divided among several of the 20-L carboys previously filled with pre-screened seawater. The number of carboys employed varied depending on the biomass of copepods being added. The labeled carboys were put back into the on-deck incubators and maintained at surface water temperatures by running seawater. The temperature variation inside the incubators was recorded by Onset Tidbit loggers. It was considered that the ship movement was sufficient to keep phytoplankton in suspension during the incubation. After 5 days (in March, April and May) and 4 days (in June/July, August and October), the carboys were filtered through 45- $\mu\text{m}$  sieves, copepods were pooled by the original size fractions and preserved immediately in 5% buffered seawater formalin as the final sample (T-5 or T-4). All preserved material was stained with Rose Bengal.

Back in the laboratory, preserved copepods were identified to species and stage, prosome lengths were digitally measured (Roff and Hopcroft, 1986), and the progression of the cohorts was determined by changes in the stage and body size. Development time was calculated as  $1/MR$ , where  $MR$  is the observed molt rate. Copepodite dry weights

were predicted from a length–weight relationship developed for *M. pacifica* in the northern Gulf of Alaska:  $\log_{10}DW = 3.29 \times \log_{10}PL - 8.75$  ( $r^2 = 0.98$ ,  $n = 83$ ), where *PL* is prosome length in  $\mu\text{m}$  and *DW* is dry weight in  $\mu\text{g}$  (Fig. 2.2). This length–weight relationship was determined by placing measured copepods in pre-weighed pans, drying at  $55^\circ\text{C}$  for 24 h, and then weighing to  $\pm 0.1 \mu\text{g}$  using a Cahn Microbalance. Single, fresh copepods, immobilized with several drops of formalin, were used for each length–weight measurement for C4–C6. Smaller stages were grouped, with up to 10 C1 of similar lengths (within  $25 \mu\text{m}$ ), and fewer C2–C3, employed for each weighing. To convert dry weight (*DW*) to carbon weight (*CW*), we used a conversion coefficient of 0.4 (Båmstedt, 1986). The instantaneous growth rates ( $\text{day}^{-1}$ ) within a given cohort over the incubation time  $t$  (days) were computed from the equation  $g = (\ln W_t - \ln W_0)t^{-1}$  where  $W_0$  and  $W_t$  are the mean dry weight of artificial cohorts at the beginning and the end of incubation period  $t$  (days), respectively (Runge and Roff, 2000).

An empirical equation to predict juvenile growth of *M. pacifica* was developed by stepwise multiple linear regression analysis, and the relative effects of initial copepodite stage, body weight, temperature, Chl *a* concentration and their interactive influences on growth rates were analyzed (SAS system V9). Non-linear models were fitted using a combination of SAS (V8) and R (V1.8.1), with equivalent  $r^2$  calculated from appropriate model sum of squares (Anderson-Sprecher, 1994). We explored the explanatory power of Chl *a* measured both within our experiments and present in the upper 30 m at the time of collection. We also compared the measured growth rates with those rates predicted by models. Growth rates were standardized to  $5^\circ\text{C}$  using  $Q_{10}$  of 2.70 for food-saturated broadcast-spawning copepods (Hirst and Bunker, 2003). For other analyses, we used the regression features within Sigmaplot (V8 & 9).

## RESULTS

### Environmental conditions

The field experiments were carried out in 4 consecutive years during the seasonal productive period in the northern Gulf of Alaska. Incubation temperature varied

seasonally similar to that of the upper mixed layer, but the differences among stations within a cruise were insignificant (Fig. 2.3). Typically, incubation temperature fell between 5 and 6°C from March to May, and increased to 10–15°C from July to October. The relatively high temperatures in 2003 were partly attributable to an atypically late cruise in May 2003.

Seasonal patterns of Chl *a* concentration within the upper 30 m were quite variable between years, but generally increased from March to April, peaked in May and declined from July to October, but remained relatively high ( $\sim 1 \text{ mg m}^{-3}$ ) and uniform across sampling stations (Fig. 2.3). The total Chl *a* measured within incubation experiments and that present in the upper 30 m at the time of collection were not significantly different except during the spring bloom when large diatoms were removed by the pre-screening process.

The seasonal partitioning of size-fractionated Chl *a* within the pre-screened seawater was variable. The larger particle Chl *a* ( $>20 \text{ }\mu\text{m}$ ) accounted for 41–46% of the total during the spring bloom (April and May) and  $\sim 20\%$  at other times. The  $\sim 0.5\text{--}5 \text{ }\mu\text{m}$  fraction averaged 25–35% of the total Chl *a* during the spring bloom and was relatively high (50–60%) during the summer and fall. The medium-size-fraction Chl *a* ( $5\text{--}20 \text{ }\mu\text{m}$ ) averaged 20–30% throughout.

### **Development and growth rate**

Copepodites C1–C5 of *M. pacifica* occurred within the upper 50 m mixed layer through all sampling seasons in the northern Gulf of Alaska, while the estimated development and growth rates exhibited a variable pattern (Fig. 2.4). Seasonally, the longest stage durations and lowest growth rates were observed in March, then growth rates increased progressively to the highest in October with corresponding short stage durations (Fig. 2.5).

C5 data were limited and contributed substantially to variability; patterns became clearer when C5 data were removed. Generally, *M. pacifica* copepodites (C1–C2) had relatively slower growth and longer stage durations in March at  $0.049 \pm 0.032 \text{ day}^{-1}$  and

25.5±4.0 days (mean ± SE), respectively, while in April copepodites (mainly C1–C4) tended to grow faster compared with the previous month. The growth rates and stage durations (mean ± SE) over 4 years in April were 0.092±0.008 day<sup>-1</sup> and 14.8±1.8 days, while the monthly mean growth rate and stage duration were not significantly different in 2001, 2002 and 2003 (Fig. 2.5). In May of 2002–2004, most copepodites from C1–C4 had shorter stage durations of 10.6±2.0 days and underwent optimal growth at 0.116±0.011 day<sup>-1</sup>. In July and August of 2003, the monthly mean growth rate and stage duration for copepodites at C1–C3 were significantly different and were more variable in July (Fig. 2.5). Seasonally, the fastest growth appeared in October in both 2002 and 2003, while it occurred during July in 2001. The monthly mean growth rate and stage duration in October of 2001–2003 were 0.153±0.021 day<sup>-1</sup> and 8.2±1.3 days (mean ± SE), respectively. The overall growth rate for all sampling seasons over the 4 years ranged from 0.004 to 0.285 day<sup>-1</sup> with mean ± SE of 0.114±0.007 day<sup>-1</sup>.

After removal of seasonal temperature influences on growth and development, the standardized growth rates over 4 years tend to decrease with increasing stage, while developmental time is slightly longer (Fig. 2.6). The mean growth rates for copepodite stage C1 in 2002 and 2003 were not significantly different, while both were significantly lower than in 2004. Over 4 years, the mean growth rate of C1 corrected to 5°C was 0.091±0.010 day<sup>-1</sup> with stage duration of 16.3±2.3 days (mean ± SE). For copepodite stage C2–C4, the growth rates after standardization were consistently higher in 2004 because of only spring data, and the slowest rates always occurred in 2003, while the rates in 2001 and 2002 were intermediate (Fig. 2.6). The growth rates and stage durations for *M. pacifica* copepodite C2 over 4 years were 0.090±0.008 day<sup>-1</sup> and 13.1±1.4 days, respectively. For copepodite stage C3, the mean growth rate and stage duration over 4 years were 0.090±0.007 day<sup>-1</sup> and 11.9±1.5 days. The growth rate started to slow down at copepodite C4 (0.054±0.009 day<sup>-1</sup>), with stage duration of 19.6±2.6 days. Stage C5 had the slowest growth at 0.023±0.009 day<sup>-1</sup> with the longest stage duration of 46.7±11.1 days. The overall mean standardized growth rate for all sampling seasons of 2001–2004 was 0.083±0.005 day<sup>-1</sup>, ranging from 0.002 to 0.185 day<sup>-1</sup>.

### Functional relationships to growth rate

Temperature and body size are two determinants of copepod growth; however, both were only modestly correlated with the growth rate of *M. pacifica* in this study.

Simple linear regression models of temperature versus growth rates were significant for C1, C2 and C3 with corresponding  $r^2$  of 0.20 ( $P=0.016$ ), 0.28 ( $P=0.002$ ) and 0.21 ( $P=0.025$ ), respectively, while these relationships were not significant for C4 and C5. Similar analysis indicated that growth rate was positively related to body size for each early copepodite stages (C1, C2, C3, and C4), but not significantly. Stepwise multiple regression analysis selected incubation temperature, Chl *a*, initial stage and body size as significant explanatory variables in the best-fitted model with  $r^2=0.42$  and  $P<0.0001$  (Table 2.1).

After removing temperature effects on growth, through  $Q_{10}$  (2.7) standardization, the growth rates of *M. pacifica* followed a significant Michaelis–Menten relationship with Chl *a* concentrations (Fig. 2.7, Table 2.1). Copepodite C1, C2 and C3 were grouped together because of their similar response curves of growth rate to Chl *a* when regressed individually. The Michaelis–Menten relationship for the group combining C4 and C5 together was also explored. The C1–C3 group and C4–C5 group exhibited a similar Michaelis–Menten relationship with Chl *a* concentration, and 35 and 45% of variance in growth was significantly explained by Chl *a* concentration, respectively. For the group combining C1–C5 together, Chl *a* still explained 28% of the variance in growth rate. Moreover, the saturated growth rate ( $g_{\max}$ ) and half-saturated Chl *a* concentration ( $K_{\text{chl}}$ ) for C1–C3 and C1–C5 groups were very similar with 0.136–0.149 day<sup>-1</sup> and 0.602–0.610 mg m<sup>-3</sup>, correspondingly. The C4–C5 group tended to be more Chl *a* dependent than earlier stages with high half-saturated Chl *a* concentration ( $K_{\text{chl}}$ ) of 1.50 mg m<sup>-3</sup> and the saturated rate of growth of 0.102 day<sup>-1</sup> (Table 2.1). The inclusion of body weight in addition to the Michaelis–Menten relationship to chlorophyll produced the most satisfying single model, accounting for 35% of the variance in growth rate for C1–C5, with  $g_{\max}$  of 0.144 day<sup>-1</sup> and  $K_{\text{chl}}$  of 0.646 mg m<sup>-3</sup>.

## DISCUSSION

### Development

To date, only a few attempts have been made in the field to estimate development time of *M. pacifica*. In most of our experiments, all stages of *M. pacifica* were present because of the overlap of three generations in this region (Batchelder, 1985). In this study, the estimated development times (corrected to 5°C) appear comparable with the few previous estimates for this species determined in the laboratory or through following natural cohorts in the field (Table 2.2). Based on this study, at 5°C, it would take ~60 days for *M. pacifica* to grow from copepodite stage C1 to C5 in the northern Gulf of Alaska, consistent with the ~65 days estimated in the laboratory (Padmavati and Ikeda, 2002), and >30–35 days estimated by natural cohort analysis during spring at colder temperatures (3–6°C) in the southeastern Bering Sea (Vidal and Smith, 1986). Taking into account this study and other field estimates of development for *M. pacifica*, such as 3–4 months in the central Gulf of Alaska (Batchelder, 1985), 2–3 months from egg hatching to C5 in the southern Japan Sea (Hirakawa and Imamura, 1993) and 2–3 months in the Oyashio region (Padmavati *et al.*, 2004), all estimates suggest that a 50–55 day generation length (including 20 days of naupliar development) in the Bering Sea (Vidal and Smith, 1986) is too fast.

Owing to our shallow daytime sampling, and the strong diel vertical migration of *M. pacifica* at older copepodite stages (Batchelder, 1985; Hattori, 1989), we were only able to sample relatively few C5s for estimating their stage duration. The reported stage duration for C5 here could be an overestimate, while it was comparable with 55 days estimated at same temperature in the laboratory (Padmavati and Ikeda, 2002). Given 25–32 days of naupliar development estimated in the laboratory at 3–9°C in this area (Pinchuk and Paul, 1998), the generation time for *M. pacifica* would be within 130–138 days, which is consistent with the 3–4 months determined in the central Gulf of Alaska (Batchelder, 1985), <167.1 days estimated in laboratory (Padmavati and Ikeda, 2002) and >2–3 months estimated in the Oyashio region (Padmavati *et al.*, 2004).

### Growth rate

To our knowledge, this study is only the second field study attempting to estimate the growth rate of *M. pacifica* in the subarctic Pacific. However, estimated rates in this study are somewhat inconsistent with the only other published rates, determined through analysis of natural cohorts during the spring in the southeastern Bering Sea (Table 2.2). In our study, most growth rates fell below the range of 0.13–0.15 day<sup>-1</sup> previously measured in the southeastern Bering Sea from March to July, and above the range reported during August and October (Fig. 2.4). Both the overall mean growth rate of 0.114 day<sup>-1</sup> and standardized rate of 0.083 day<sup>-1</sup> over 4 years appear slower in this area compared with those in the Bering Sea. This difference could be explained by differences in food and temperature conditions between these two studies. Generally, the southeastern Bering Sea is a food-rich region (Fig. 3 in Vidal and Smith, 1986), compared with the coastal Gulf of Alaska (Fig. 2.3). In April and May, temperature differences are minimal, so food concentration must be the main determinant of the difference of growth rates for both regions. During summer (July and August), the growth of large-sized copepods in this study may be suboptimal under conditions of relatively low food concentration and high temperature, because the critical food concentration required for large copepods increases with temperature (Vidal, 1980). In this sense, unsurprisingly, our estimates and standardized growth rates tend to be lower than those in the southeastern Bering Sea.

Nonetheless, growth rates estimated in this study are comparable with those of other calanoid species in the Gulf of Alaska (Table 2.3). The standardized rate of 0.083 day<sup>-1</sup> for *M. pacifica* tends to be slightly slower than that of 0.105 day<sup>-1</sup> for *Neocalanus flemingeri/plumchrus* (Liu and Hopcroft, 2006), 0.118 day<sup>-1</sup> for *Calanus marshallae* (H. Liu and R. R. Hopcroft, unpublished data), and close to the rates of 0.08 day<sup>-1</sup> for *Centropages abdominalis* (Slater and Hopcroft, 2005) and 0.074 day<sup>-1</sup> for *Calanus pacificus* (H. Liu and R. R. Hopcroft, unpublished data). Given the relatively constant temperature and rich food conditions during the spring bloom in the Gulf of Alaska (in April and May), it is reasonable to expect relatively high rates for *N.*

*flemingeri/plumchrus* and *C. marshallae* for which rate measurements have been made principally during that period. In contrast, the standardized growth rates of *M. pacifica* are averaged over longer periods which include the lower productivity periods in the summer and fall, and are (not surprisingly) lower. It is interesting to note that the overall uncorrected mean juvenile growth rate of  $0.114 \text{ day}^{-1}$  over 4 years for *M. pacifica* is very close to the  $0.10 \text{ day}^{-1}$  rate for egg production estimated concurrently in 2002 (Hopcroft *et al.*, 2005), likely due to the similar food and temperature conditions in the two studies.

### **Growth rate and its determinants**

In general, the rates of copepod growth are most strongly affected by temperature (McLaren, 1978; Huntley and Lopez, 1992), food concentration (Vidal, 1980; Kimmerer and McKinnon, 1987) and additionally by body size (Hirst and Lampitt, 1998; Hopcroft and Roff, 1998; Hopcroft *et al.*, 1998; Richardson and Verheye, 1999; Hirst and Bunker, 2003). In most cases, the interactive effects between temperature, food concentration and body size are confounded (Vidal, 1980; Hirst and Bunker, 2003). In this study, temperature has been shown as a significant determinant of growth rate in statistical analysis (Table 2.1). In aquatic ecosystems, Chl *a* has long been considered a general index of food concentration, although it may be a poor predictor for some species (Hirst and Bunker, 2003; Bunker and Hirst, 2004). In this study, its significant relationship with growth rate suggests that Chl *a* is a reasonable food index for copepodites of *M. pacifica*, and in particular the early copepodites. After removing the effect of temperature, the standardized growth rates for late stages (C4–C5) are more food dependent than for earlier stages (C1–C3) in this study, possibly due to the increasing critical food concentration for growth with increasing body size observed in the laboratory (Vidal, 1980), and the food-limited growth more likely encountered by larger copepods in the field (Hopcroft *et al.*, 1998). Typically, *M. pacifica* mainly prey on phytoplankton during bloom conditions (Batchelder, 1986; Padmavati *et al.*, 2004). However, other studies on feeding appendages and gut contents suggest that *M. pacifica* might tend to be omnivorous when phytoplankton becomes scarce and be capable of feeding on



dinoflagellates, tintinnids, radiolarians, copepod nauplii and detritus (e.g. Haq, 1967; Sullivan *et al.*, 1975; Batchelder, 1986; Hattori, 1989; Padmavati *et al.*, 2004; Halsband-Lenk, 2005), and these food sources become more important after the spring bloom (Padmavati *et al.*, 2004). Given a long life span of multiple generations coexisting together, the diel vertical migration and a relatively short period of phytoplankton blooms in this study area, *M. pacifica* will encounter variability and variety in food items, and this no doubt accounts for the high degree of scatter in the chlorophyll relationship, especially at the lower chlorophyll concentrations outside the spring bloom (Fig. 2.7).

Globally, the rates of copepod growth are negatively correlated with body size (Hirst and Lampitt, 1998; Hirst and Bunker, 2003). However, a positive relationship between growth rate and body size within each copepodite stage was observed for *N. flemingeri/plumchrus* in the field (Liu and Hopcroft, 2006); for *M. pacifica*, a similar pattern is suggested but is not significant. Under favorable food conditions, animals within a stage that are growing rapidly tend to be larger in size than those growing slowly (Liu and Hopcroft, 2006). The relatively constant temperature and optimal food conditions experienced during spring made this pattern clear for *N. flemingeri/plumchrus*, but feeding history and diet shifts occurring over spring through fall likely make this pattern unclear for *M. pacifica*. Here, we suggest it is premature to make this observation a “rule”, and more laboratory and field observations are still required. In contrast, across stages, it appears that growth declines on average with increasing stage under most field conditions.

### **Comparison to global models**

No matter what method is utilized for estimating copepod growth rate, all of the traditional methods share common drawbacks of being time consuming and labor intensive. This limits the availability of growth rate data for specific species within given areas and favors the use of synthesis approaches (e.g. Huntley and Lopez, 1992; Hirst and Shearer, 1997; Hirst and Lampitt, 1998; Hirst and Bunker, 2003). Modeling is appealing in that copepod growth rates can be predicted over large spatial and temporal scales on

the basis of a few easily measurable parameters (temperature, body weight and food source), particularly where no directly measured growth rates are available. Global models should be highly representative for a range of species living in broad ecosystem types. Therefore, it is useful to explore the utility of these models for species in specific study cases. A comparison of our measured rates with the rates predicted from models was consistent with previous cases attempting to test these models (Peterson *et al.*, 2002; Rey-Rassat *et al.*, 2004). Generally, the temperature-dependent model (Huntley and Lopez, 1992) appears overestimated, and the temperature-body weight model (Hirst and Lampitt, 1998) results in a more adequate match (Fig. 2.8). Surprisingly, for early stages C1–C3, the predictions by the temperature-dependent model match direct measurements very well (Table 2.4) in part because the earlier stages may in general experience less food-limitation (e.g. Hopcroft *et al.*, 1998).

Although the temperature–body weight model (Hirst and Lampitt, 1998) is, on average, more predictive than the temperature-dependent model, this model tends to underestimate when growth rates are high and overestimate when growth rates are low (Fig. 2.8). More recent models, which incorporate temperature, body weight and Chl *a* (Hirst and Bunker, 2003), come closer to our direct measurements of *M. pacifica* in the case of their ‘adult broadcast spawners’ and ‘all-data’ models, but their ‘juvenile broadcast spawners’ model results in 4–10-fold overestimation. Similar comparative patterns of agreement emerged in our comparison of these models with direct measurements for *N. flemingeri/plumchrus* (Liu and Hopcroft, 2006). Clearly, lack of good agreement is in part due to the lack of somatic growth rate data for species in subarctic waters. Therefore, some caution should be taken when using rates predicted by these models.

Clearly, more growth data that cover various ecosystem types are required for refining these models, especially for species living in cold waters (e.g. the subarctic Pacific). Advances in methodology are anticipated, which will generate more precise data (e.g. RNA/DNA, enzymes, molecular probes), but more time is needed to make them feasible and routine (Saiz *et al.*, 1998; Yebra and Hernández-León, 2004; Yebra *et al.*, 2005).

Until new methods under development come into use, the artificial-cohort method is the only technique that can be routinely employed at sea and simultaneously executed on all dominant species, regardless of its time and labor-intensive requirements post-cruise. Its utility for somatic growth determination has been proven for *M. pacifica*, as well as for other species living in this area (Liu and Hopcroft, 2006).

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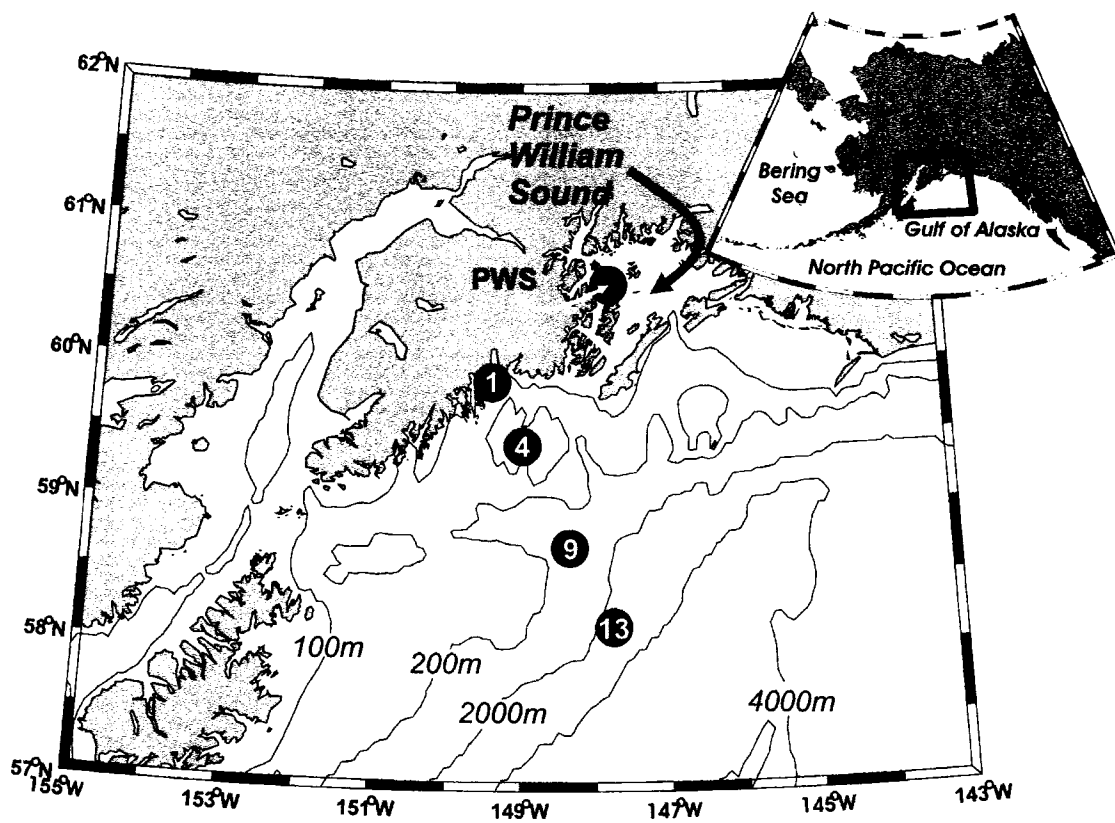
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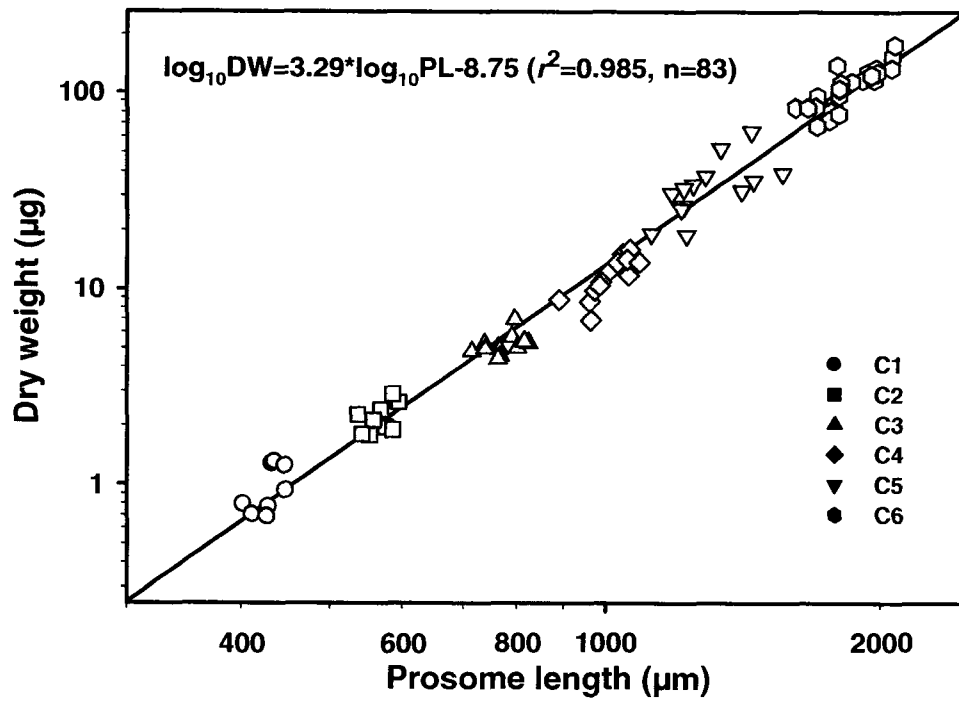
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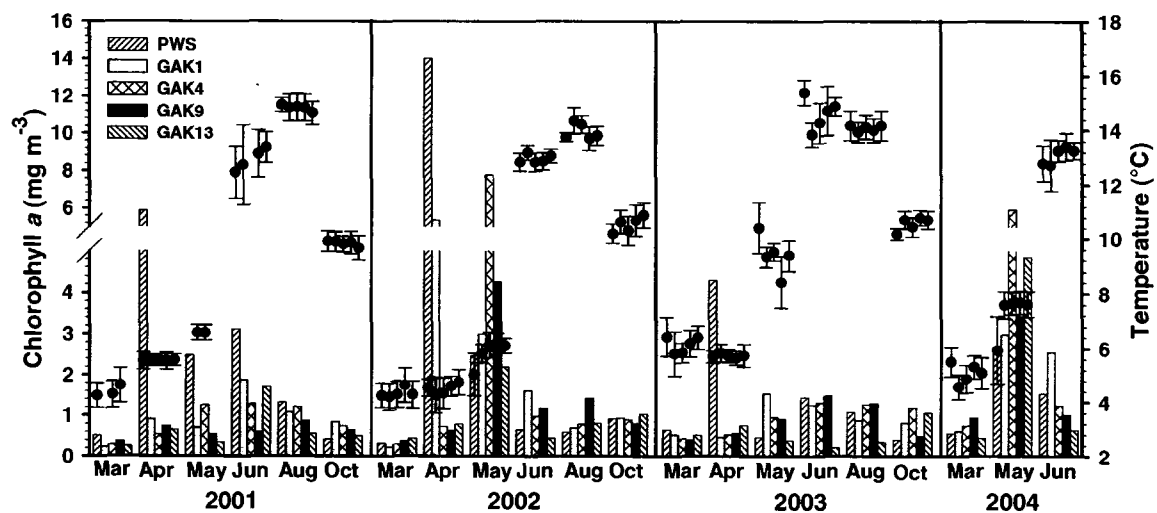
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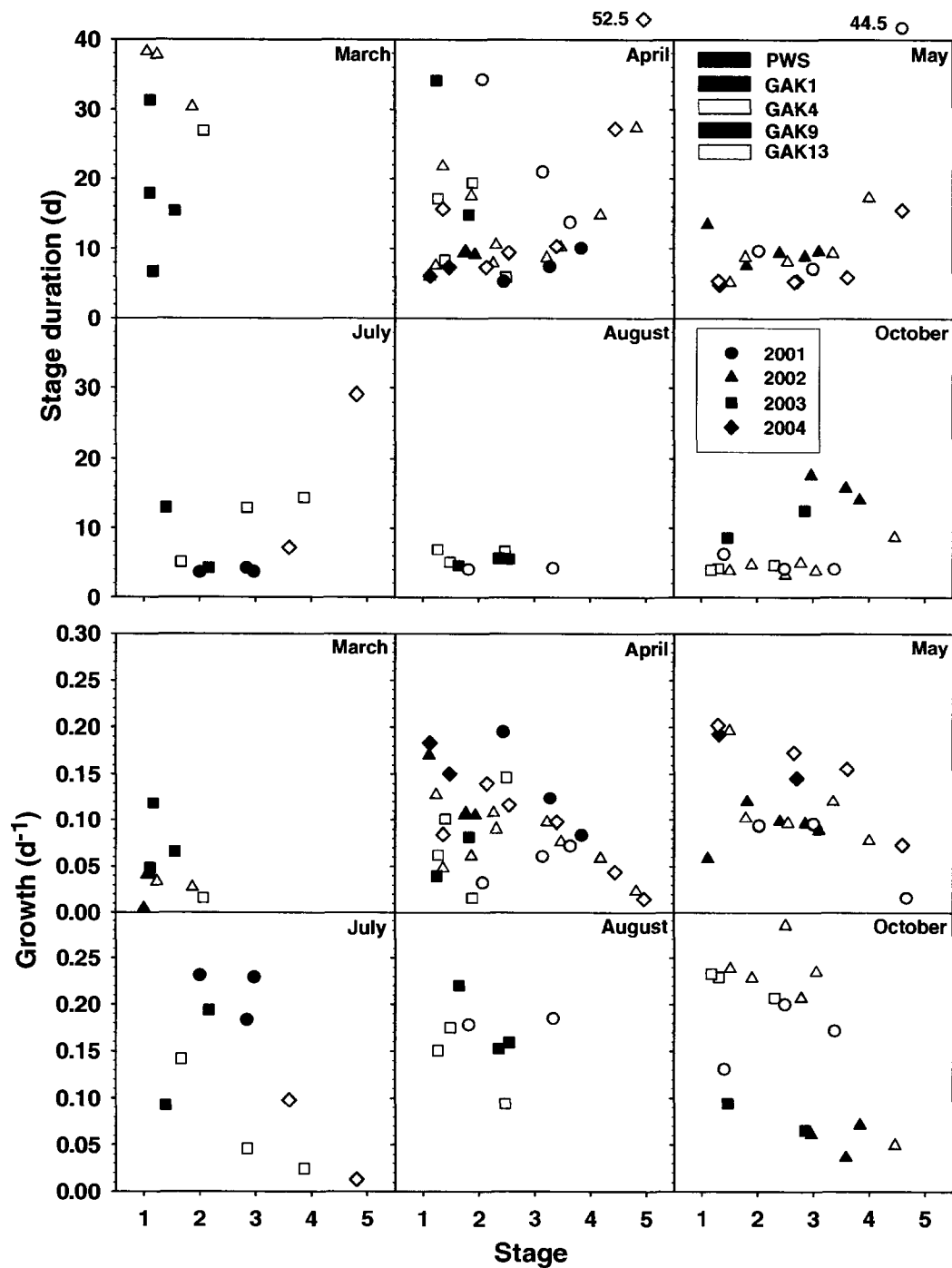
**Figure 2.1** Map of the sampling area in the northern Gulf of Alaska.



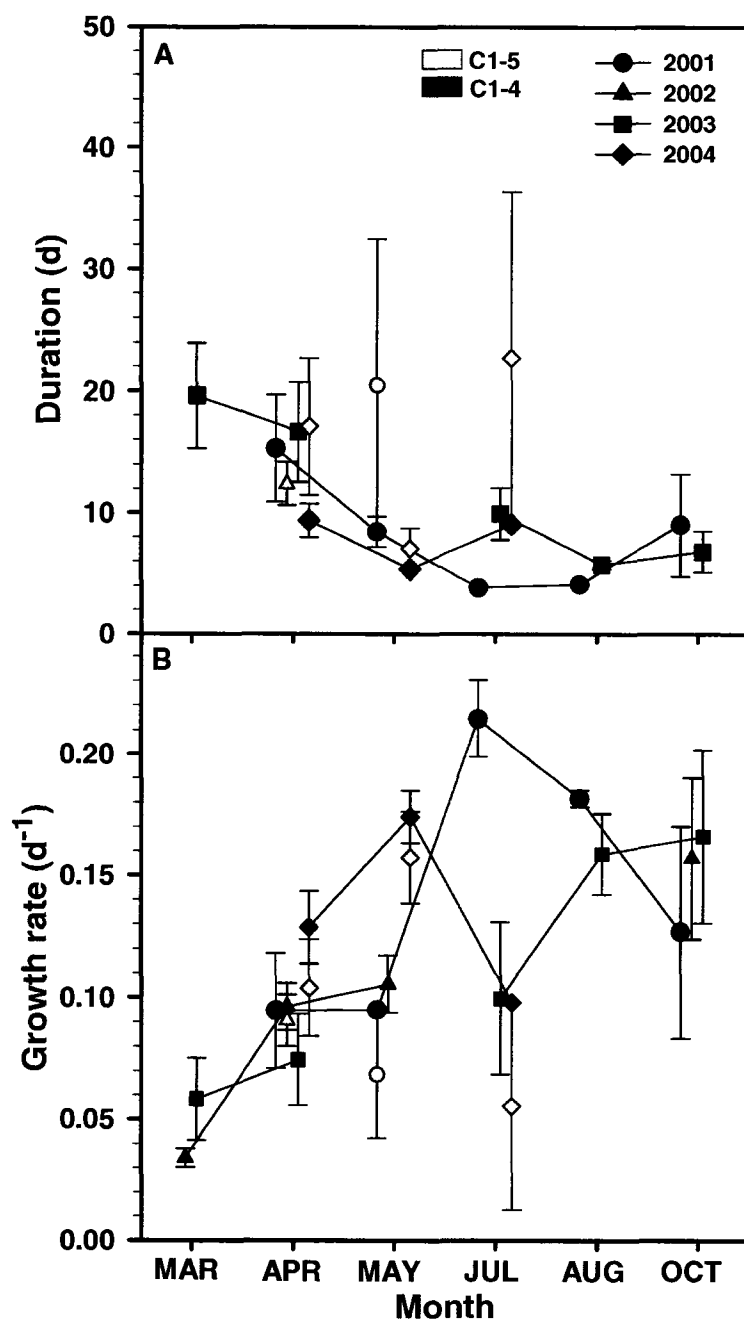
**Figure 2.2** Relationship between prosome length (PL, μm) and dry weight (DW, μg) for *Metridia pacifica* stages C1–C6 in the northern Gulf of Alaska.



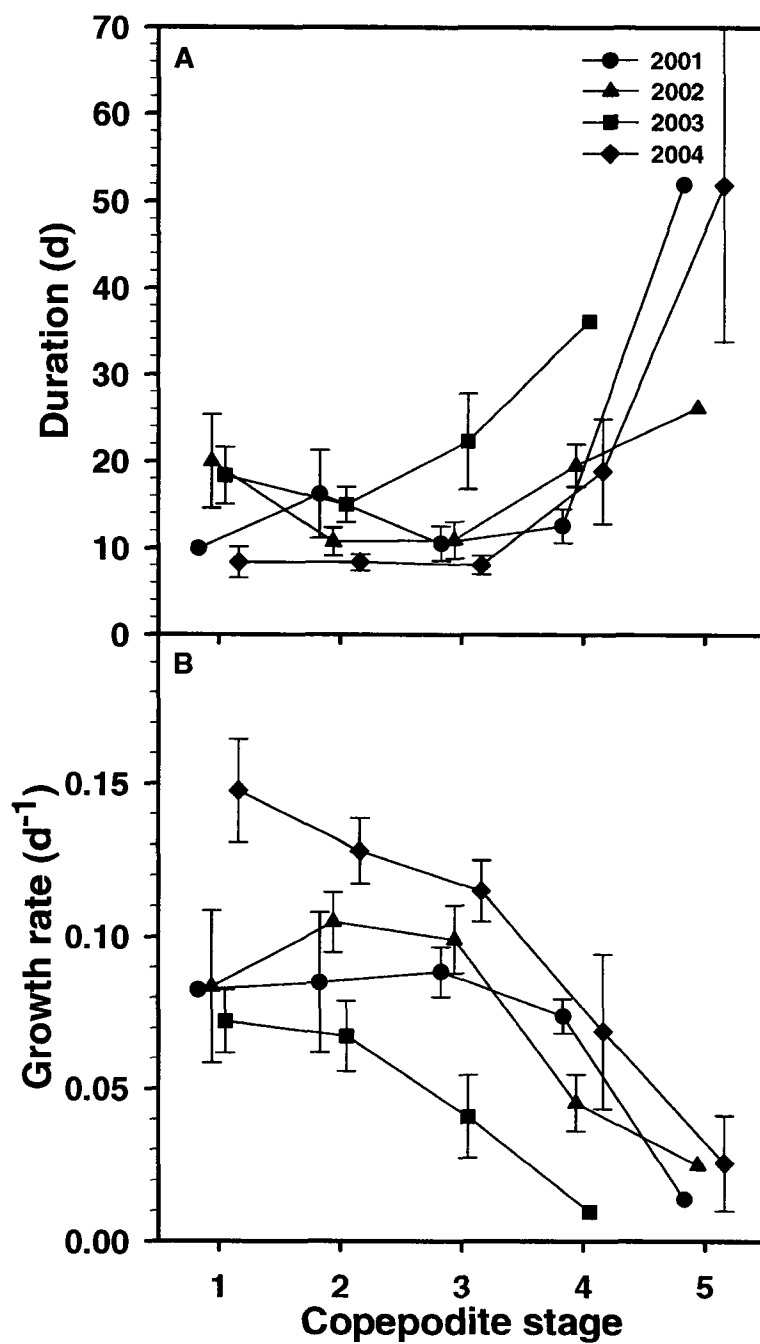
**Figure 2.3** Total chlorophyll *a* concentration at study sites averaged over the upper 30 m (bars) and incubation temperatures of experiments at sea in the northern Gulf of Alaska 2001–2004 (circles). Error bars are standard deviations.



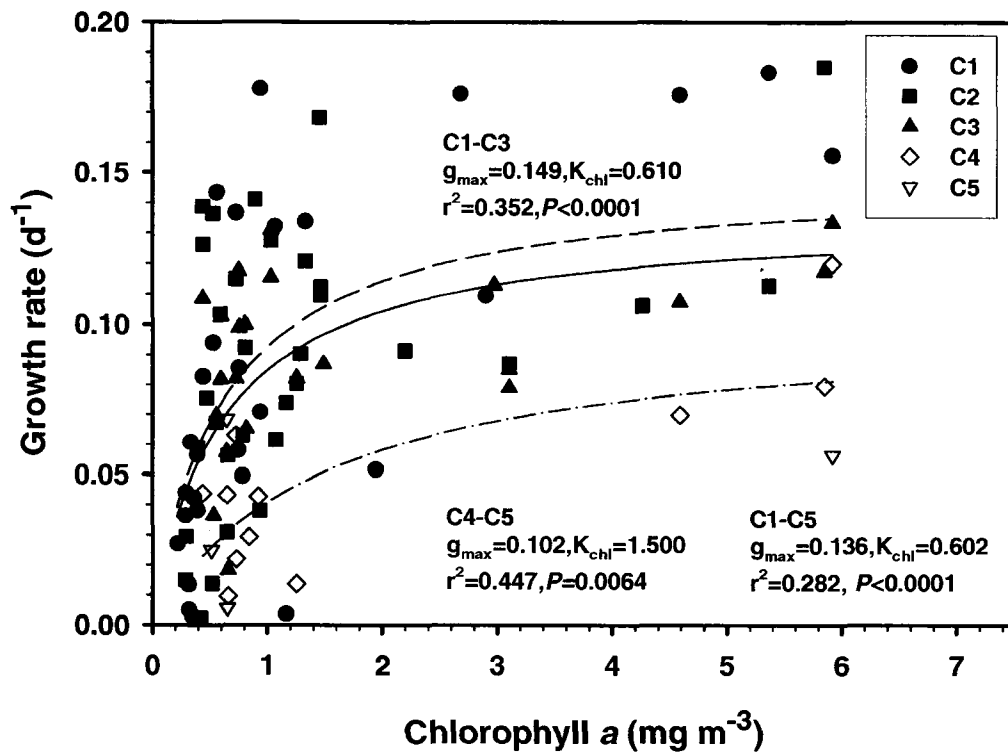
**Figure 2.4** Stage durations (upper panels) and growth rates (lower panels) of *Metridia pacifica* in the northern Gulf of Alaska 2001–2004. Stage is the average of the population at start of the incubation.



**Figure 2.5** Seasonal mean stage duration and growth rate of *Metridia pacifica* copepodite in the northern Gulf of Alaska 2001–2004. Values plotted against initial stage and offset in time to improve interpretation. Error bars are standard errors.

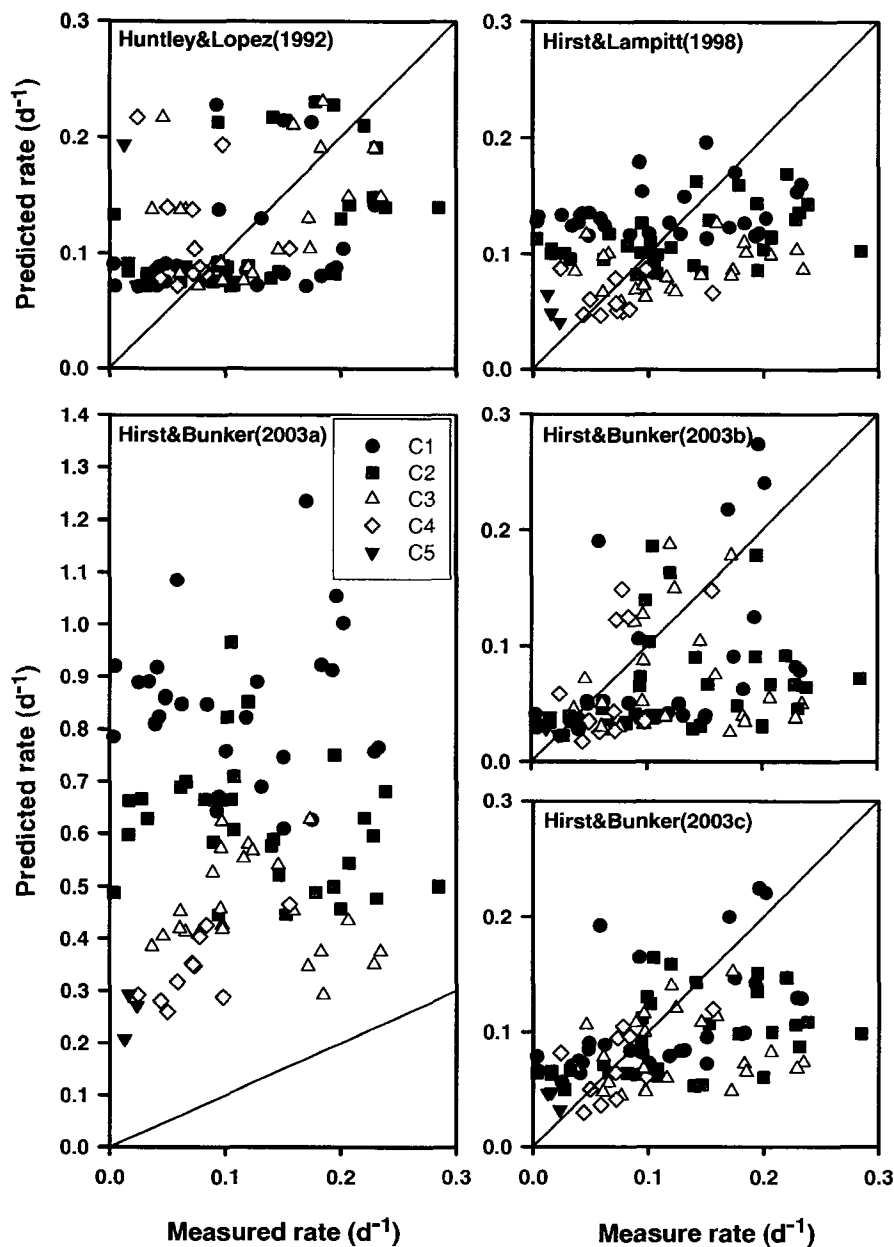


**Figure 2.6** Mean stage duration and growth rate both corrected to 5°C for *Metridia pacifica* in the northern Gulf of Alaska 2001–2004. Values plotted against initial stage and offset in time to improve interpretation. Error bars are standard errors.



**Figure 2.7** Functional relationships between temperature-corrected growth rates and total chlorophyll *a* for *Metridia pacifica* in the northern Gulf of Alaska. Michaelis-Menten curves fitted for C1–C5 (solid line), for C1–C3 (dashed line), and C4–C5 (dashed dot line).





**Figure 2.8** Comparisons of the measured growth rates for *Metridia pacifica*, and growth rates predicted from the models of Huntley and Lopez (1992), Hirst and Lampitt (1998), and Hirst and Bunker (2003). Hirst and Lampitt (1998) equation for all data equation (adults and juveniles of both broadcast and sac-spawners) and Hirst and Bunker (2003): a, for juveniles broadcasters; b, for adult broadcasters; c, for all data combined.

**Table 2.1** Functional relationships of *Metridia pacifica* between growth rate ( $Gr$ ,  $g \text{ day}^{-1}$ ), initial stage ( $Stg$ ), incubation temperature ( $T$ ,  $^{\circ}\text{C}$ ), body weight ( $\mu\text{g C individual}^{-1}$ ) and total chlorophyll  $a$  concentration ( $Chl$ ,  $\mu\text{g l}^{-1}$ ) in the northern Gulf of Alaska

Function	Equation	n	T ( $^{\circ}\text{C}$ )	Coefficients ( $p$ )					$r^2(p)$
Multiple Regression	$Gr = a_1 + a_2T + a_3 \log Chl + a_4 \log BW + a_5 Stg$	98	4.1-14.7	$a_1$ 0.4033 ( $<0.0497$ )	$a_2$ 0.0095 ( $<0.0001$ )	$a_3$ 0.0549 (0.0012)	$a_4$ 0.3689 (0.0021)	$a_5$ -0.1694 (0.0006)	0.425 ( $<0.0001$ )
Michaelis-Menten	$g = Chl[g_{\max}]/(Chl + K_{ch})$ (C1-C5)	98	5		$g_{\max}$ 0.136 ( $<0.0001$ )		$K_{ch}$ 0.602 (0.0005)		0.282 ( $<0.0001$ )
Michaelis-Menten	$g = Chl[g_{\max}]/(Chl + K_{ch})$ (C1-C3)	83	5		$g_{\max}$ 0.149 ( $<0.0001$ )		$K_{ch}$ 0.610 (0.0003)		0.352 ( $<0.0001$ )
Michaelis-Menten	$g = Chl[g_{\max}]/(Chl + K_{ch})$ (C4-C5)	15	5		$g_{\max}$ 0.102 (0.0011)		$K_{ch}$ 1.500 (0.1089)		0.447 (0.0064)
Composite Nonlinear	$g = a * \log BW + Chl[g_{\max}]/(Chl + K_{ch})$ (C1-C5)	98	5	$a$ -0.0301 (0.0015)		$g_{\max}$ 0.144 ( $<0.0001$ )		$K_{ch}$ 0.646 ( $<0.0001$ )	0.354 ( $<0.0001$ )

**Table 2.2** Comparison of growth rates and development times (in parenthesis) for *Metridia pacifica* in the subarctic Pacific

Location	Temp (°C)	Growth rate and developmental time							Source
		Egg- N6	C1	C2	C3	C4	C5	Average	
Gulf of Alaska	5.0		0.091 (16.3)	0.090 (13.1)	0.090 (11.9)	0.054 (19.6)	0.023 (46.7)	0.083 (21.5)	This study
Southeastern Bering Sea	0.5-		0.13-	0.13-	0.13-	0.13-	0.13-	0.13-0.15	Vidal and Smith(1986)
	6.0	(~20)	0.15 (6-7)	0.15 (6-7)	0.15 (6-7)	0.15 (6-7)	0.15 (6-7)	(6-7)	
Hokkaido Japan	5.0	(47.3)	(14.2)	(11.9)	(16.2)	(22.5)	(55)	(23.96)	Padmavati and Ikeda(2002)
Gulf of Alaska	3.0- 9.0	(25- 32)							Pinchuk and Paul(1998)

**Table 2.3** Standardized growth rate of *Metridia pacifica* to 5°C using  $Q_{10}$  (2.7) compared with other dominant species in the northern Gulf of Alaska

Species	Temp (°C)	Growth rate	Egg production rate	Location	Source
<i>Metridia pacifica</i>	5.0	0.083		Gulf of Alaska	This study
<i>Metridia pacifica</i>	5.0		0.10	Gulf of Alaska	Hopcroft <i>et al</i> (2005)
<i>Metridia okhotensis</i>	5.0		0.11	Gulf of Alaska	Hopcroft <i>et al</i> (2005)
<i>Neocalanus flemingeri/plumchrus</i>	5.0	0.105		Gulf of Alaska	Liu and Hopcroft (2006)
<i>Centropages abdominalis</i>	5.0	0.08		Gulf of Alaska	Slater and Hopcroft (2005)
<i>Calanus marshallae</i>	5.0	0.118		Gulf of Alaska	Liu and Hopcroft (unpublished)
<i>Calanus pacificus</i>	5.0	0.074		Gulf of Alaska	Liu and Hopcroft (unpublished)

**Table 2.4** Comparison of growth rates (at temperature 4.2–14.7°C) predicted by global models with measured rates of *Metridia pacifica* in the northern Gulf of Alaska

Model	Temperature (°C)	Percent of predicted to rates measured in this study					
		C1	C2	C3	C4	C5	C1-C5
Huntley and Lopez (1992)	4.2-14.7	100%*	96%*	93%*	172%	368%	103%
Hirst and Lampitt (1998)	4.2-14.7	129%	90%*	64%*	93%*	163%	76%*
Hirst and Bunker (2003)a	4.2-14.7	794%	510%	346%	494%	890%	434%
Hirst and Bunker (2003)b	4.2-14.7	67%*	58%	53%	91%*	169%	62%*
Hirst and Bunker (2003)c	4.2-14.7	99%*	78%*	63%*	98%*	177%	72%*

\* non-significant at  $\alpha=0.05$ , two sample, two tail t-Test assuming unequal variance.

In Hirst and Bunker (2003), a: for juvenile broadcasters; b: for adult broadcasters; c: for all data.

**Chapter 3****A comparison of seasonal growth and development of the copepods  
*Calanus marshallae* and *C. pacificus* in the northern Gulf of Alaska\***

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## ABSTRACT

The juvenile growth rates and development times of subarctic *Calanus marshallae* and temperate *C. pacificus* were investigated May through October of 2001–2004 in the northern Gulf of Alaska. The relationships between prosome length (PL,  $\mu\text{m}$ ) and dry weight (DW,  $\mu\text{g}$ ) for copepodite C2–C6 of *Calanus marshallae* and C1–C6 of *C. pacificus* were  $\log_{10}DW=4.304\times\log_{10}PL-11.561$ , and  $\log_{10}DW=4.001\times\log_{10}PL-11.304$ , respectively. The copepodite stage durations ranged from 3–16 days for *C. marshallae*, and 3–23 days for *C. pacificus*. Seasonally, growth rates increased from May to October, typically ranging between 0.055 and 0.291  $\text{day}^{-1}$  with mean of  $0.170\pm0.008 \text{ day}^{-1}$  (SE) for *C. marshallae*, while growth rates increased from August to October between 0.018 and 0.296  $\text{day}^{-1}$  with mean of  $0.142\pm0.016 \text{ day}^{-1}$  (SE) for *C. pacificus*. After standardization to 5°C ( $Q_{10}$  of 2.7), growth rate averaged  $0.118\pm0.007 \text{ day}^{-1}$  and  $0.074\pm0.009 \text{ day}^{-1}$  for *C. marshallae* and *C. pacificus*, respectively, and was significantly correlated ( $r^2=0.55$ ) to chlorophyll *a*, with saturated growth rates of 0.223  $\text{day}^{-1}$  for *C. marshallae*. Despite their different geographic ranges, growth rates of the two species appear to have similar functional responses to chlorophyll *a*, and body size, with temporal and spatial differences in occurrence responsible for apparent differences in mean rates. Measured juvenile growth rates of the two *Calanus* species in this study were comparable to other calanoid species in this area, and showed reasonable agreement to global *Calanus* growth models, but more limited agreement with global copepod growth models, suggests that further refinement of these models is required.

**Key words:** *Calanus marshallae*, *Calanus pacificus*, growth, development, Gulf of Alaska

## INTRODUCTION

Copepods constitute the major component of the zooplankton community in marine ecosystems, and are of vital importance to the flow of matter and energy, material flux to the ocean's interior, and retention of nutrients within the euphotic layer (Banse, 1995). Our understanding of the functioning of marine ecosystems ultimately relies on precisely measured rate processes, particularly those of the copepods that dominate planktonic communities (Longhurst, 1984). Growth is among these key process rates determining the roles of copepods in the trophodynamics of marine ecosystems (Kiørboe, 1997). Thus, over the past few decades, the estimation of growth and reproductive rates of copepods has become a central aspect of marine plankton research (Runge and Roff, 2000). Secondary production is then estimated by integrating the product of specific growth rates with their biomass (Poulet *et al.*, 1995; Runge and Roff, 2000).

Measuring *in situ* somatic growth rates of juvenile copepods is time consuming and labor intensive; moreover, unbiased measurements of copepod growth are difficult to obtain in the field. Traditionally, the "egg production rate" has been considered as a proxy for the juvenile growth rate assuming that adult body mass remains in steady-state and adult females' net growth is equal to the amount of material expelled as eggs (e.g. Sekiguchi *et al.*, 1980; McLaren and Corkett, 1981; Runge and Roff, 2000). Increasingly, this assumption has been challenged (Hopcroft and Roff, 1998a; Richardson and Verheye, 1998; Hirst and McKinnon, 2001), because the *in situ* growth rates of adults and juveniles have been frequently found food-limited under various natural conditions (Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Hopcroft and Roff, 1998a; Liu and Hopcroft, 2006a). Moreover, the females' fecundity is more likely subjected to food limitation than juvenile growth (Kiørboe, 1997), so it is no longer reliable to derive juvenile growth rates from the rates of egg production.

At present, our knowledge of juvenile copepod growth rates in nature has been predominantly limited to tropical and temperate waters, as indicated by recent synthesis (Hirst and Lampitt, 1998; Hirst and Bunker, 2003), and there is a conspicuous deficiency of data in subpolar and polar waters. Almost no vital rates exist for the common copepod



species characteristic of the entire subarctic Pacific, except for recent efforts in the northern coastal Gulf of Alaska (Liu and Hopcroft, 2006a, b). The lack of directly measured growth rates fosters the widespread use of global models of copepod growth, although the adequacy of such models has not been fully established (Richardson *et al.*, 2001; Peterson *et al.*, 2002; Rey-Rassat *et al.*, 2004; Liu and Hopcroft, 2006a, b). Clearly, more direct measurements are necessary to refine our understanding of global patterns.

The species of genus *Calanus* are abundant members in the zooplankton community in most ocean waters (Brodsky, 1972; Bradford and Jillett, 1974). Across the subarctic Pacific, *Calanus marshallae* and *C. pacificus* are the two predominant sibling species, and both have multi-generational annual life cycles (Conover, 1988). Typically, *C. marshallae* is present in the neritic zooplankton assemblage from spring to winter over the northern Gulf of Alaska shelf, while *C. pacificus* occurs inshore mostly during the summer (Incze *et al.*, 1997; Coyle and Pinchuk, 2003, 2005). From late spring to early winter, these two species contribute important secondary production after the departure of larger-bodied *Neocalanus* species from the upper layer. To the north, *C. marshallae* is a key species in the Bering Sea (Napp *et al.*, 2002; Baier and Napp, 2003), accounting for up to 63% of the diet of juvenile walleye pollock during the summer (Grover, 1991). To the south, *C. pacificus* is considered a key species in the California Current system (e.g. Rebstock, 2001; Peterson and Keister, 2003).

Despite their prevalence, to date we have only a few direct measurements of the juvenile growth of *C. marshallae* and *C. pacificus*, all made with different approaches: *C. marshallae* stages C1–C3 using the natural cohort method in the southeastern Bering Sea (Vidal and Smith, 1986), C1–C5 using the molt-rate method off the Oregon coast (Peterson *et al.*, 2002), plus extensive laboratory rearing of *C. pacificus* (Vidal, 1980a, b; Landry 1983) and *C. marshallae* (Peterson, 1979, 1986). Notably, the studies on *C. marshallae* off Oregon do not encompass the temperature range this species typically occupies in subarctic waters. The objectives of this study are threefold: to fill the gap of juvenile growth rates of *C. marshallae* and *C. pacificus* in the northern Gulf of Alaska; explore the seasonal relationships between growth rate and food availability, temperature

and body size; and compare our measured rates with rates predicted by the globally applicable models.

## METHOD

Sample collections and experimental work in this study were conducted during the U.S. GLOBEC program, Long-Term Observation Program in the Coastal Gulf of Alaska (see Weingartner *et al.*, 2002). The sampling area is characterized by a shelf of 100–300 m depth, with complex bathymetry and many deep-water coastal fjords and embayments (Fig. 3.1). There were six cruises per year from 2001–2003 in March, April, May, June/July, August, and October. In 2004, only three cruises were conducted in March, May and July. Experimental work was set up at four Gulf of Alaska (GAK) stations along the Seward line from inshore to just past the shelf break (i.e. GAK1, 4, 9, 13), plus one station along the western inner Knight Island Passage of Prince William Sound (either KIP2 or PWS2) where the depth is 500–800 m (Fig. 3.1). Water samples for assessment of ambient phytoplankton concentration at these stations were collected at multiple depths using 5 L Niskin bottles on a CTD rosette, serially size-fractionated using 20  $\mu\text{m}$  Poretics, 5  $\mu\text{m}$  Nuclepore and GF/F filters, with frozen samples later analyzed fluorometrically for chlorophyll *a* concentration (Stockwell and Whitley, unpublished data).

Experimental methodology is identical to that employed successfully for *Neocalanus* and *Metridia pacifica* in this region (Liu and Hopcroft, 2006a, b). Seawater for incubations at each station was collected by replicate CTD casts with a 12 place rosette of 10 L Niskin bottles equipped with 9 mm valves. Collections were typically made within the upper mixed layer, usually from 5 to 20 m depth, but at inshore (GAK 1) and PWS stations, the depths for seawater collection were occasionally deepened to avoid salinities of less than 30 caused by melting snow and glaciers. Incubation seawater was pre-screened through 100  $\mu\text{m}$  Nitex mesh sacs placed over the ends of Tygon tubing while siphoning the bottles into 20 liter soft-walled carboys. Once filled, carboys were stored in large insulated fish tubs ( $\sim 1 \text{ m}^3$  capacity) rigged as flow-through incubators and equipped

with a fenestrated lid that reduced lighting to ~20% of ambient surface illumination. Food concentrations of incubation seawater at the beginning and the end of experiments were measured as size-fractionated chlorophyll *a* using the same protocols and fluorometric techniques employed for monitoring activities.

At each of the experimental stations, copepods were collected using a 64  $\mu\text{m}$  plankton net with 4 L cod-end fished slowly from the surface to 50 m, and back to the surface (~20  $\text{m}^3$  of water) between 0800 and 1200 hrs. Immediately upon retrieval, copepod collections were diluted using the pre-screened seawater and placed into an incubator at ambient surface water temperatures. Soon after, copepods were sorted into “artificial cohorts” (Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Hopcroft and Roff, 1998b; Hopcroft *et al.*, 1998) by sequential passage through submerged screens of the following mesh sizes: 1300, 1000, 800, 600, 500, 400, 300, 200, 150, and 100  $\mu\text{m}$ . The sample was constantly diluted with pre-screened water cooled to ambient seawater temperature, and as each cohort size-class was created, it was placed into an incubator at ambient seawater temperature. Under ideal conditions, this cohort-creating process took 1 hr and as much as 3 hrs when chains of large filamentous algae were abundant.

Prior to incubation, each size-fraction was gently homogenized and evenly divided. One half was concentrated and preserved in a 5% buffered seawater formalin as the time zero sample (T-0), and the other half equally divided among several of the 20 L carboys previously filled with pre-screened seawater. The number of carboys employed varied depending on the biomass of copepods being added. The labeled carboys were put back into the on-deck incubators, and maintained at surface water temperatures by running seawater. The thermal variation inside the incubators was recorded by Onset Tidbit loggers. Ship movement was sufficient to prevent algal cells from coagulating and sinking during the incubation. After 5 days (in March, April and May) or 4 days (in June/July, August and October) the carboys were filtered through 45  $\mu\text{m}$  sieves, and copepods were pooled by the original size fractions and then preserved immediately in 5% buffered seawater formalin as the final sample (T-5 or T-4). All preserved material was stained with Rose Bengal.

Back at the laboratory, the preserved samples were identified to species and stage based on the morphological features given for copepodite stages of *C. marshallae* and *C. pacificus* (Frost, 1974; Peterson, 1979). Prosome lengths were measured with computer assistance (Roff and Hopcroft, 1986), and the progression of the cohorts was determined by changes in the stage and body size. Weights were predicted using the relationships between prosome length (PL) and dry weight (DW) created in the northern Gulf of Alaska for *C. marshallae*:  $\log DW = 4.034 \times \log PL - 11.561$  ( $r^2 = 0.958$ ,  $n = 57$ ), and for *C. pacificus*:  $\log DW = 4.001 \times \log PL - 11.304$  ( $r^2 = 0.953$ ,  $n = 62$ ), where PL is in  $\mu\text{m}$ , and DW is in  $\mu\text{g}$  (Fig. 3.2). Carbon weights were calculated assuming 40% carbon content for copepods (Båmstedt, 1986).

Development time was calculated as  $1/\text{MR}$ , where MR is the observed molting rate of each cohort. This approach may be subject to some errors (Hirst *et al.*, 2005), because we frequently lacked concurrent site experiment-specific molt rates for adjoining cohort “stages”, and because our experiments typically contain a mixture of multiple stages, the modified molt rate (MMR) method was not employed. The growth rate ( $\text{day}^{-1}$ ) within a given cohort over the incubation time  $t$  (days) was computed from the equation  $g = (\ln W_t - \ln W_0) t^{-1}$ , where  $W_0$  and  $W_t$  are the mean dry weight of artificial cohorts at the start and the end of incubation period  $t$  (days) (Runge and Roff, 2000). Recent concerns over growth rate errors using the molt rate method (Hirst *et al.*, 2005) are not operational in this study, because we employ incubation periods not development time to estimate our growth rates. Some bias and “noise” may exist in our estimates because we have used weight predicted from length-weight analysis rather than direct measurements of weights (Kimmerer *et al.*, in press), and this is unavoidable by our methods. The impacts may be greatest for later stages where both “structural” growth and lipid accumulation occur concurrently, and variably, in *Calanus* species (e.g. Campbell *et al.*, 2001; Rey-Rassat *et al.*, 2002).

We explored the explanatory power of chlorophyll *a* measured both within our experiments and present in the upper 30 m at the time of collection. Multiple linear regression analysis was used to explore the functional relationship of growth rate to

copepodite stages, incubation temperatures, chlorophyll *a* concentration and body weight, using the SAS system (V9). The best fitted model was determined based on the  $R^2$  and  $C_p$ . A composite nonlinear model incorporating the body size with the traditional Michaelis-Menten relationship was developed using a combination of SAS (V8) and R (V1.8.1) (Liu and Hopcroft, 2006b), with equivalent  $R^2$  calculated from appropriate model sum of squares (Anderson-Sprecher, 1994). For other regression analyses and figure preparation Sigmaplot (V9) was used. When necessary, growth rates and stage durations were normalized to 5°C to facilitate comparison to other species in this region, and to 10°C to facilitate comparison to other studies, using a  $Q_{10}$  of 2.70 for food-saturated broadcast-spawning copepods (Hirst and Bunker, 2003).

## RESULTS

### Temperature and chlorophyll *a* concentration

The incubation temperature exhibited a seasonal signal with temperature rising in late spring, peaking in late summer and dropping back in fall (Fig. 3.3), consistent with seasonal thermal cycles in the northern Gulf of Alaska (see Coyle and Pinchuk, 2005). Within each cruise, the temperature differences between stations were insignificant (Fig. 3.3). Typically, incubation temperature was 5–6°C from March to May, but increased to 10–15°C from July to October. The relatively high temperatures in 2003 were due to an atypically late cruise in May of 2003, and the abnormally warm sea water temperatures of that year.

Seasonal patterns of chlorophyll *a* concentration within the upper 30 m were quite variable between years, but generally increased from March to April, peaked in May, then declined from July to October, but remained relatively high ( $\sim 1 \text{ mg m}^{-3}$ ) and uniform across sampling stations (Fig. 3.3). The total amount of chlorophyll *a* concentration measured within incubation experiments and present in the upper 30 m mixed layer at the time of collection were not significantly different (paired *t*-test,  $\alpha=0.05$ ), except during the spring bloom when large diatoms were removed by the pre-screening process. The seasonal partitioning of size-fractionated chlorophyll *a*

concentration within the prescreened seawater was variable. The larger particle chlorophyll *a* ( $>20\ \mu\text{m}$ ) averaged 41–46% of the total during the spring bloom (April and May), and around 20% at other times; the  $\sim 0.5\text{--}5\ \mu\text{m}$  fraction accounted for 25–35% of the total chlorophyll *a* concentrations within the spring bloom, and was relatively high (50–60%) during summer and fall; the medium size chlorophyll *a* ( $5\text{--}20\ \mu\text{m}$ ) averaged 20–30% throughout the sampling seasons.

### **Growth rate and development time of *Calanus marshallae* and *C. pacificus***

The occurrences of *Calanus marshallae* and *C. pacificus* tend to be seasonal in this study (Fig. 3.4). The copepodite stages of *C. marshallae* were rare in March and April, common in May, and then became less common through the summer to fall, while *C. pacificus* were more common during August to October in the northern Gulf of Alaska (Fig. 3.4).

For both species, the estimated growth rate and stage duration were variable; however both species shared a similar pattern, that is, growth rate decreases with the increase of copepodite stage (Fig. 3.4). Seasonally, the stage duration and growth rate of copepodites for *C. marshallae* were relatively less variable compared to *C. pacificus* (Fig. 3.5, Table 3.1). Visually, the mean monthly stage duration of *C. marshallae* tended to decline, while the growth rate increased through May to October (Fig. 3.6). Generally, the stage duration and growth rate in May over four years were 7.3 days and  $0.174\ \text{day}^{-1}$ , respectively. The average stage duration in July and August of 2002–2003 decreased to 6.9 days with growth rate of  $0.174\ \text{day}^{-1}$ , and 6.2 days with corresponding growth rate of  $0.181 \pm 0.022\ \text{day}^{-1}$ , respectively. The shortest seasonal stage duration and the fastest growth occurred in October with 5.7 days and  $0.191\ \text{day}^{-1}$ . However, these monthly mean differences were not significant except for the estimated stage durations of  $10.4 \pm 1.1$  days (mean  $\pm$  SE) in July of 2002, and  $6.2 \pm 0.6$  days in May of 2004, for which the corresponding growth rates were  $0.093 \pm 0.003\ \text{day}^{-1}$ , and  $0.131 \pm 0.017\ \text{day}^{-1}$ , respectively. The overall mean stage duration and growth rates of *C. marshallae* in this study were 7.0 days and  $0.176 \pm 0.008\ \text{day}^{-1}$ , respectively.

The copepodites of *C. pacificus* were more common in August and October (Fig. 3.4). Similar to *C. marshallae*, the stage duration of *C. pacificus* appeared to be shorter, while growth rate tended to be faster, from August to October in 2002–2003. However the pattern appeared more variable in August than in October with inclusion of data in 2001 and 2004 (Fig. 3.5, Table 3.1). Generally, over the study years the average stage duration and growth rate in August were 8.2 days and  $0.119 \text{ day}^{-1}$  respectively, while in October, the stage duration and growth rate were 7.2 days and  $0.182 \text{ day}^{-1}$ , respectively. The overall mean stage duration and growth rates of *C. pacificus* in this study were 7.8 days and  $0.142 \pm 0.016 \text{ day}^{-1}$ , respectively.

After standardization to  $5^{\circ}\text{C}$ , stage duration and growth rate exhibited a similar tendency for both *C. marshallae* and *C. pacificus*, with stage duration increasing slightly with development stage. Growth rate noticeably slowed with the increase of developmental stages, although for *C. pacificus* this pattern was more variable compared to *C. marshallae* (Fig. 3.6, Table 3.2). The average standardized stage duration and growth rates for C1 copepodite of *C. marshallae* over 3 years were 9.4 days and  $0.157 \text{ day}^{-1}$ . For copepodites at C2, the standardized stage duration was 8.7 days with growth rate of  $0.145 \text{ day}^{-1}$ . For C3 and C4 copepodite the standardized stage durations tended to be longer: about 11 and 18.7 days respectively, while growth rates slowed from  $0.109 \text{ day}^{-1}$  to  $0.057 \text{ day}^{-1}$ , correspondingly. The mean  $5^{\circ}\text{C}$  standardized stage duration for all observations of *C. marshallae* was 11.9 days and growth rate was  $0.117 \pm 0.007 \text{ day}^{-1}$ .

For *C. pacificus*, the changes in standardized stage duration and growth rate were similar to those of *C. marshallae*, i.e., the standardized growth rate tended to slow with increasing stage and development time became slightly lengthened. Generally, for C1 of *C. pacificus*, the averaged stage duration and growth rate standardized at  $5^{\circ}\text{C}$  over 4 years were 12.0 days and  $0.106 \text{ day}^{-1}$  respectively. The stage duration and growth rate for C2 were 7.2 days and  $0.147 \text{ day}^{-1}$  respectively. With increasing stages, the development and growth rates slowed to 7.7 days and  $0.117 \text{ day}^{-1}$  for C3, 11.4 days and  $0.088 \text{ day}^{-1}$  for C4, and 22.6 days and  $0.027 \text{ day}^{-1}$  for C5, respectively. The overall mean  $5^{\circ}\text{C}$  standardized stage duration for *C. pacificus* was 15 days and growth rate was  $0.074 \pm 0.009 \text{ day}^{-1}$ .

### Analysis of growth rate and other factors

For both species temperature failed to be a simple explanatory variable of growth rate, but growth rate was better correlated with body size after removing the temperature effect for both *C. marshallae* ( $r^2=0.19$ ,  $P<0.0001$ ) and *C. pacificus* ( $r^2=0.67$ ,  $P<0.0001$ ; Fig. 3.7). For *C. marshallae*, the best fitted multiple regression model contained temperature, chlorophyll *a*, body size and stage as significant explanatory variables ( $r^2=0.594$ ,  $P<0.0001$ ) (Table 3.3). However, the attempt to fit a similar model for *C. pacificus* was unsuccessful, likely due to the limited range of temperature and chlorophyll *a* present in *C. pacificus* observations.

After standardization to 5°C ( $Q_{10}$  of 2.7), the growth rates of *C. marshallae* were significantly related to chlorophyll *a* in the form of a Michaelis-Menten relationship (Fig. 3.7, Table 3.3). Chlorophyll *a* concentration exhibited the same explanatory power in the fitted Michaelis-Menten model for the standardized growth rates at 5 and 10°C with  $r^2=0.337$  and  $P<0.0001$  (Table 3.3). The saturated growth rate ( $G_{\max}$ ) and half saturated food concentration ( $K_{\text{chl}}$ ) were 0.223 day<sup>-1</sup> and 1.538 mg m<sup>-3</sup> at 5°C, and 0.366 day<sup>-1</sup> and 1.534 mg m<sup>-3</sup> at 10°C, respectively. A composite nonlinear model incorporating body size with the Michaelis-Menten relationship accounts for up to 54.6% of the variance in the standardized growth rate at 5 and 10°C ( $P<0.0001$ ). Moreover, within this model body size was negatively related to growth rate across chlorophyll *a* concentrations. The estimated saturated growth rate ( $G_{\max}$ ) and the half saturated food concentration ( $K_{\text{chl}}$ ) in the composite model were 0.241 day<sup>-1</sup> and 1.072 mg m<sup>-3</sup> at 5°C, and 0.395 day<sup>-1</sup> and 1.072 mg m<sup>-3</sup> at 10°C, respectively. Interestingly, the estimated saturated growth rate ( $G_{\max}$ ) in the composite model was slightly faster than its counterpart in the Michaelis-Menten relationship even under a relatively low half-saturated food concentration ( $K_{\text{chl}}$ ) (Table 3.3).

To work around the problem of limited temperature and chlorophyll range in the *C. pacificus* data, we combined data from both species and re-ran simple Michaelis-Menten and composite nonlinear models. We found the parameterization and variability explained in both models were similar to those obtained by modeling *C. marshallae*



alone, indicating that the two species have the same functional responses, because otherwise parameters would change and explained variability would decline (Fig. 3.7; Table 3.3, 3.4).

## DISCUSSION

### **Growth and development of *Calanus marshallae* and *C. pacificus***

*Calanus marshallae* and *C. pacificus* are two common species overlapping in distribution across the northern Gulf of Alaska, particularly in summer. This paper is the first attempt to examine the growth and development of these two important copepod species, and to explore the underlying relationship between growth rate and other factors based on a multiple-year field approach. Understanding the differential response of these species to environmental variables will help provide insight on how long-term climate shifts might impact their prevalence and productivity in the Gulf of Alaska and adjoining regions.

Based on this study, it initially seemed that *C. marshallae* grew and developed faster than *C. pacificus* with or without seasonal thermal influences. However, the similar functional responses of growth rate for both *C. marshallae* and *C. pacificus* in two different model analyses indicates that the observed discrepancy in growth rate between *C. marshallae* and *C. pacificus* was an artifact of the different space, time and hence environmental conditions in their data sets (i.e. not an inter-species difference).

Generally, *C. marshallae* are herbivorous copepods (Vidal and Smith, 1986; Peterson, 1986), and predominantly occur in the late spring and early summer during the bloom in the Gulf of Alaska (Coyle and Pinchuk, 2003, 2005). During that time, the chlorophyll *a* concentration and water temperature are favorable for newly recruited young, as well as old, copepodites to grow and develop close to their maximum rate (Fig. 3.4, 3.5). In terms of the food conditions, it is important to note that chlorophyll *a* is not always an accurate measure of food availability; but here chlorophyll *a* as a proper food indicator for *C. marshallae* has been proven significant, particularly if body size is considered (Table 3.3, 3.4).

For *C. pacificus*, most of the younger copepodites occur in the winter or early spring, while later stages occur in the summer in this region (Incze *et al.*, 1997). In this study the majority of data for *C. pacificus* were collected from the later copepodite stages during the summer and fall. Under warm temperatures and low food conditions (measured as chlorophyll *a*), the growth and development of later stages of *C. pacificus* are possibly sub-optimal due to food-limitation (Vidal, 1980a, b). Recent studies show that late stage and adult *C. pacificus* feed on a mixture of microzooplankton (e.g. *Protoperidinium* spp., *Gyrodinium* species) at periods when there is low abundance of phytoplankton prey (Leising *et al.*, 2005; Pierson *et al.*, 2005). This kind of omnivorous feeding in *C. pacificus*, in conjunction with limited chlorophyll range, could contribute to the lack of a chlorophyll *a* relationship in this study.

So far, several extensive studies on growth and development of *C. marshallae* have been made off the Oregon coast using laboratory approaches (Peterson, 1986, 1988; Peterson *et al.*, 2002) and in the southeastern Bering Sea (Vidal and Smith, 1986) using field approaches. Typically, our temperature-corrected growth rate and development time were consistent with these previous results at similar temperature conditions (Table 3.5). This is surprising, because the persistent coastal down-welling in the northern Gulf of Alaska (Weingartner *et al.*, 2002), should frequently lead to sub-optimal feeding conditions for *C. marshallae* compared to the food-rich regions in the southeastern Bering Sea and off the Oregon coast up-welling zone. In this study, most data on growth and development of *C. marshallae* were collected from the early copepodites (C1–C4), during the spring bloom with abundant food concentration, and this no doubt contributes to the similarity between rates in the Gulf of Alaska and Oregon. However, when temperature differences are considered, conditions in the Bering Sea appear even more optimal.

Several dominant copepod species coexist in the northern Gulf of Alaska. Our estimated growth rates for *C. marshallae* and *C. pacificus* are reasonably comparable with those of other calanoid copepods concurrently estimated in this region (Table 3.6). The relatively high standardized rate of  $0.118 \text{ day}^{-1}$  for *C. marshallae* is similar to the

0.107 day<sup>-1</sup> of *Neocalanus flemingeri/plumchrus* at 5°C (Liu and Hopcroft, 2006a), mainly because both species principally occur in the spring with similar rich food and favorable temperature conditions. Meanwhile, the growth rate 0.074 day<sup>-1</sup> for *C. pacificus* is closer to the 0.083 day<sup>-1</sup> for *Metridia pacifica* (Liu and Hopcroft, 2006b) which is based on year-round observations. Both appear to be lower than the laboratory rate of 0.141 day<sup>-1</sup> determined for the coastal species *Centropages abdominalis* (Slater and Hopcroft, 2005).

### **Relationship between growth and temperature, food condition and body size**

Copepod growth is strongly influenced by temperature (e.g. Vidal, 1980a, Huntley and Lopez, 1992), chlorophyll *a* (e.g. Vidal, 1980a; Kimmerer and McKinnon, 1987), and body size (e.g. Vidal, 1980a), with growth rates synergistically affected by the combinations of these determinants (Hirst and Lampitt, 1998; Hopcroft *et al.*, 1998; Richardson and Verheye, 1998; Hirst and Bunker, 2003; Bunker and Hirst, 2004; Liu and Hopcroft, 2006a, b). This synergistic effect was clear from our statistical analysis, with temperature, chlorophyll *a*, body size, and development stages together accounting for about 60% of the variability in the growth rate for *Calanus marshallae* (Table 3.3).

Generally, rates of copepod growth tend to be negatively related to body size (Hirst and Lampitt, 1998; Hopcroft *et al.*, 1998; Hirst and Bunker, 2003); however, thermal variation can make this size-dependent relationship unclear (Vidal, 1980a; Hopcroft *et al.*, 1998). Although *Calanus* temperature-corrected growth rate declined with increasing stage (Fig. 3.7), when stage was also employed as a parameter statistical analysis suggested a positive correlation between growth rate and body size and a negative relationship to stage (Table 3.3). The interactive influence between temperature, chlorophyll *a*, and body size on copepod growth rate has been demonstrated in the laboratory (Vidal, 1980a). In the field a positive correlation between the temperature-corrected growth rate and body size within each stage has only recently been demonstrated, for *Neocalanus flemingeri/plumchrus* in this study region under the optimal food conditions during the spring bloom (Liu and Hopcroft, 2006a). This kind of

positive relationship is also suggested visually for *C. marshallae* and *C. pacificus* here; however, none of them are significant (Fig. 3.7). Unlike *Neocalanus flemingeri/plumchrus*, the lack of pure stages in each experiment for *Calanus marshallae* blurs such patterns.

Globally, a significant Michaelis-Menten relationship exists between chlorophyll *a* and the growth rate of copepods after removing the temperature effect (Hirst and Bunker, 2003). This general pattern was also followed by *C. marshallae* in this study, with 33.7% explained variance in growth rate (Table 3.3); however, the synergistic effect between chlorophyll *a* and body size still confounds the relationship with growth. Based on this evidence, a composite nonlinear model combining body size into the traditional Michaelis-Menten function was first developed for *Metridia pacifica* (Liu and Hopcroft, 2006b). Fitting this model greatly enhanced the explainable variance in the growth rate by over 20% for *C. marshallae*, demonstrating that the composite nonlinear model is more predictive than its prototype (Table 3.1). Similar use of the composite nonlinear model only resulted in a 7% increase for *Metridia pacifica* (Liu and Hopcroft, 2006b) and insignificant improvement (~1%) for *Neocalanus flemingeri/plumchrus* in the same study area. The wide range of chlorophyll *a* concentration experienced by *C. marshallae* accentuated the interaction between food concentration and body size on growth rate that has been demonstrated previously (e.g. Vidal, 1980a; Hopcroft *et al.*, 1998).

### **Comparison with global models**

The results in this study complement the two recent studies to test the global models of copepod growth rate in the high latitudes waters of the northern Gulf of Alaska (Liu and Hopcroft, 2006a, b). All of the previous multi-species global models can be highly biased for the two *Calanus* species in this study area (Fig. 3.8, 3.9; Table 3.7), similar to the recent findings for two other dominant copepod species in this area, e.g. *Neocalanus flemingeri/plumchrus* and *Metridia pacifica*. Variable agreement in our study area is also consistent with previous efforts in other waters to test the Hirst and Lampitt (1998) models (Richardson *et al.*, 2001; Peterson *et al.*, 2002; Rey-Rassat *et al.*, 2004). Detailed

discussions on comparing models of Huntley and Lopez (1992), Hirst and Lampitt (1998), and Hirst and Bunker (2003) can be found in our previous studies (Liu and Hopcroft, 2006a, b) and is not repeated here.

Although some of the limitations of the general broadcast models (Hirst and Bunker, 2003) might be attributed to the wide mixture of species within them, one would expect such modeling approaches are more successful if restricted to a single species or genus. The two Michaelis-Menten relationships developed specifically for *Calanus* spp. (Hirst and Bunker, 2003), provide the opportunity for additional comparisons between them and this study's *C. marshallae* and *C. pacificus* rates. After correcting our data with the same  $Q_{10}$  values employed in their study, we find more reasonable agreement with their juvenile *Calanus* spp. relationship (Fig. 3.9). The poor agreement to their adult *Calanus* spp. relationship is expected, because adult growth is generally lower than that of juveniles (e.g. Hopcroft and Rolf, 1998a; Hirst and Bunker, 2003). Notably, their model for *Calanus* juveniles predicts a much narrower range of growth rates, and some tendency to overestimate at low growth rate and underestimate when rates are high. A further analysis of growth rates at each developmental stage suggests that the global model for juvenile *Calanus* spp. at 15°C can match reasonably well with our measured rates for both *Calanus* species, but a large discrepancy occurs for later copepodite stages (Table 3.3). Overall, this suggests reasonable consistency in functional response across the genus. If this is true, temperature tolerance/preference may play a primary role in determining the spatial and temporal distribution of *Calanus* species, as has been suggested for other congeners generally (e.g. Halsband-Lenk *et al.*, 2002).

Inevitably, all models have limitations and some discrepancy between measured and predicted values will occur for any single species at a specific region. Recent critical examination of the mathematical underpinning of copepod growth rate methodologies (Hirst *et al.*, 2005; Kimmerer *et al.*, in press) suggest a wide range of biases may be pervasive in much of the existing literature (including this study) that need to be resolved, and this further hampers our ability to find “global” patterns. An important finding in this study, together with our two recent studies, is to remind us that we still need direct

measurement of copepod growth rates, especially for ecosystems and species currently lacking this kind of information. Copepod growth rates are a fundamental parameter for further analysis of the flows of energy and matter through marine ecosystems. Significant errors in estimating secondary production arising from the use of biased growth data and/or inappropriate models could have large consequences in quantifying the linkage of copepods to both higher and lower trophic levels, and how this might be altered by short-term and long-term climate change.

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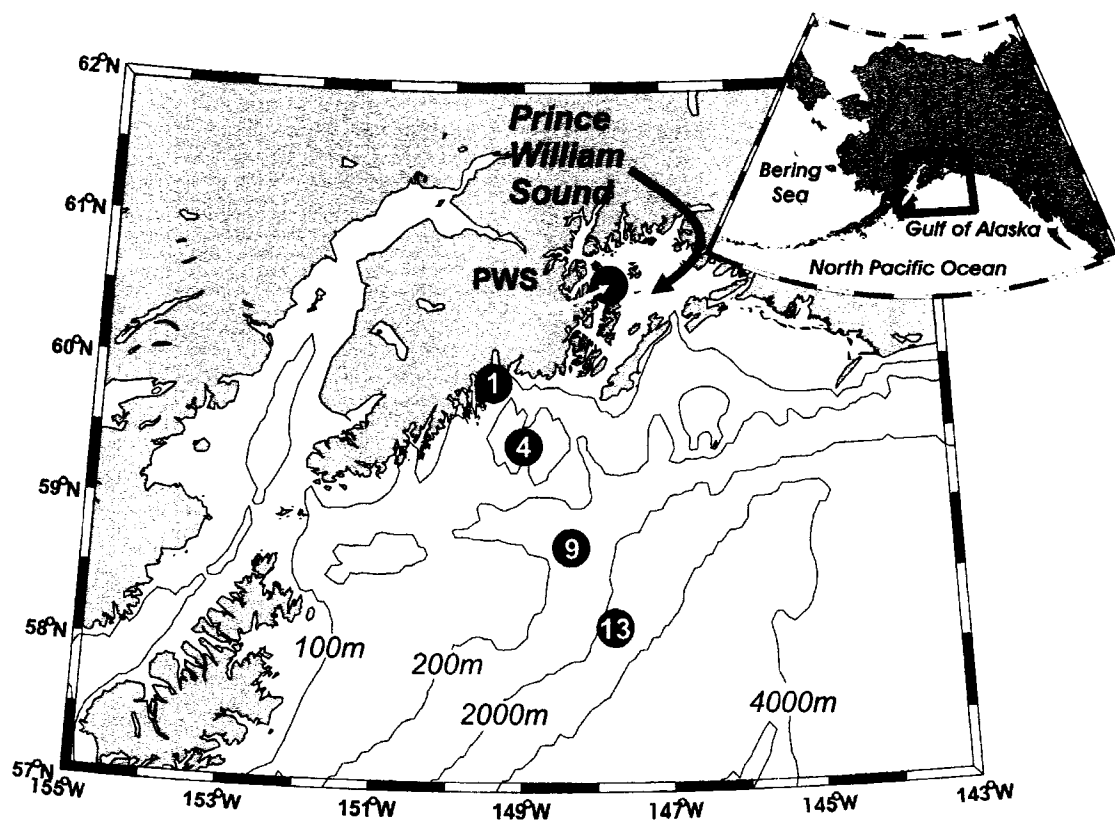
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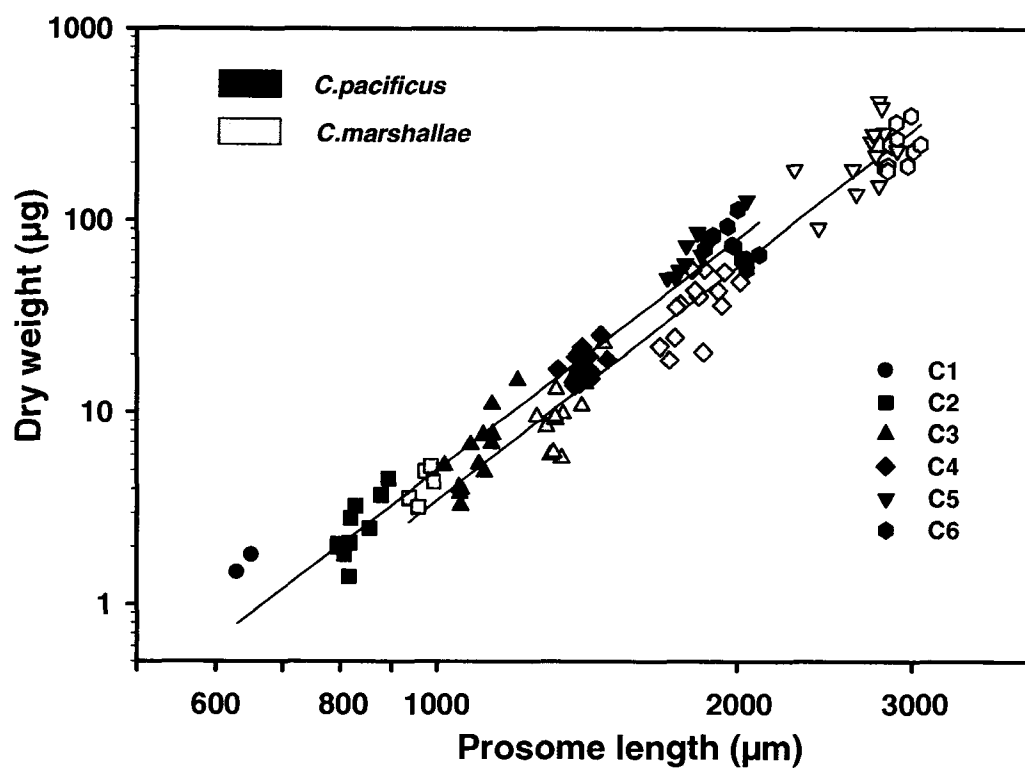
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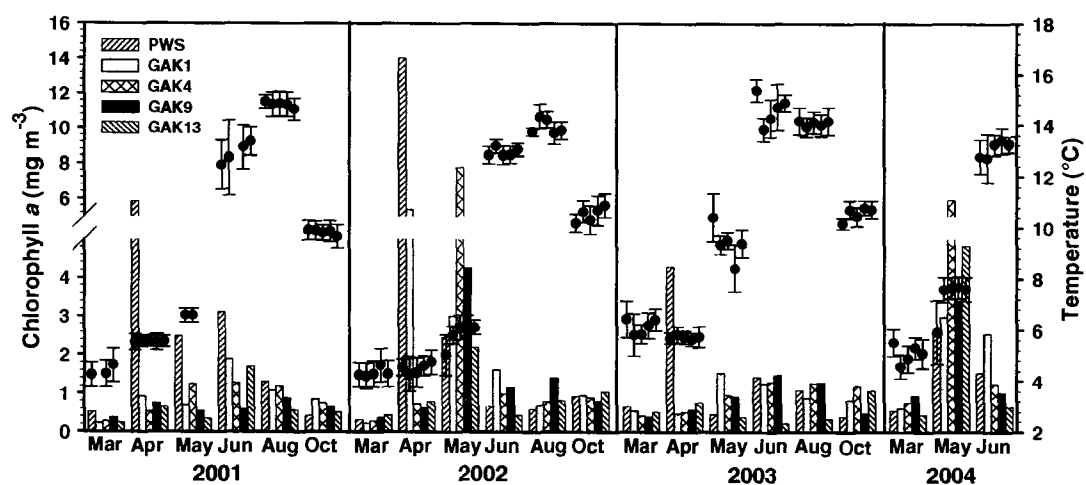
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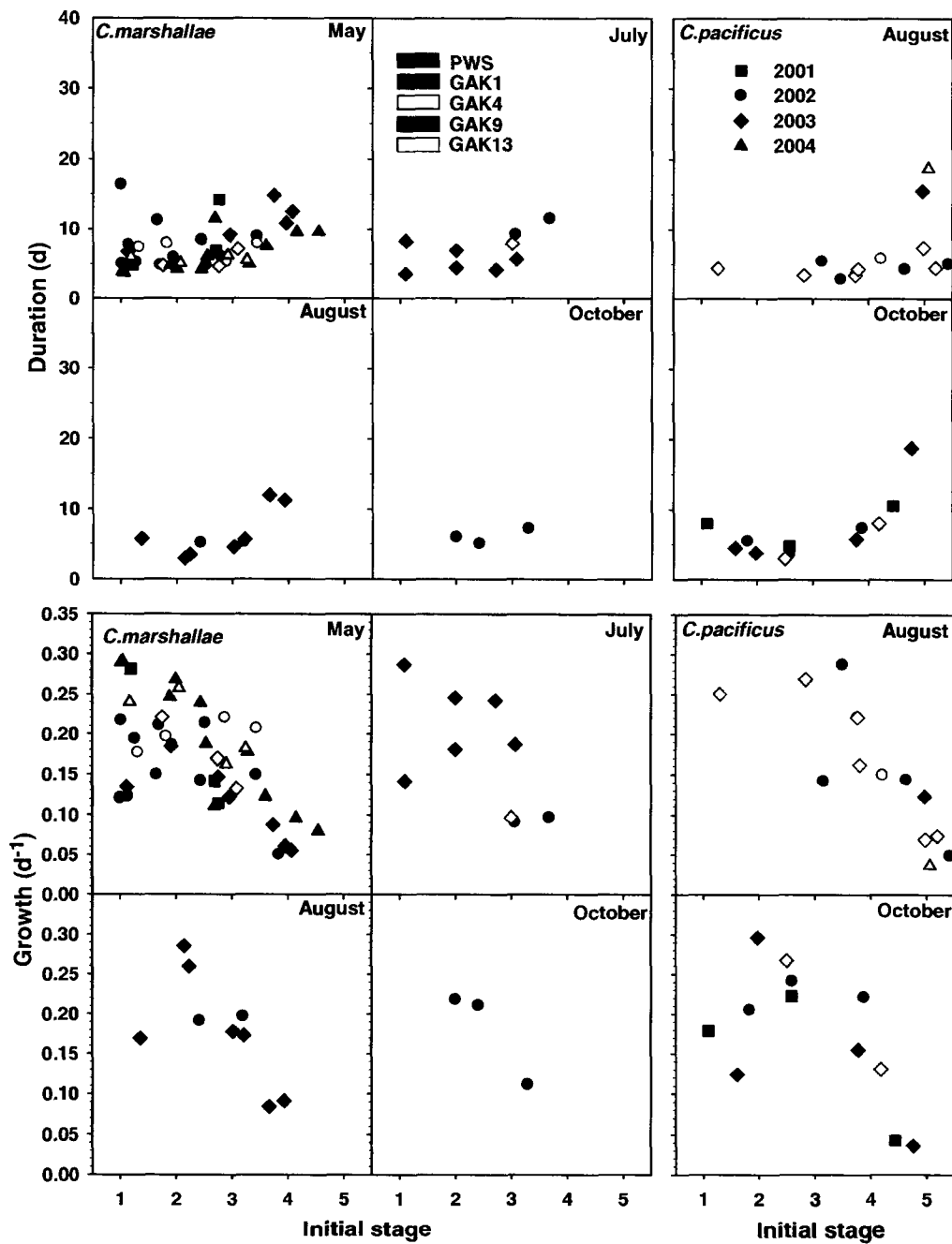
**Figure 3.1** Map of the sampling area in the northern Gulf of Alaska.



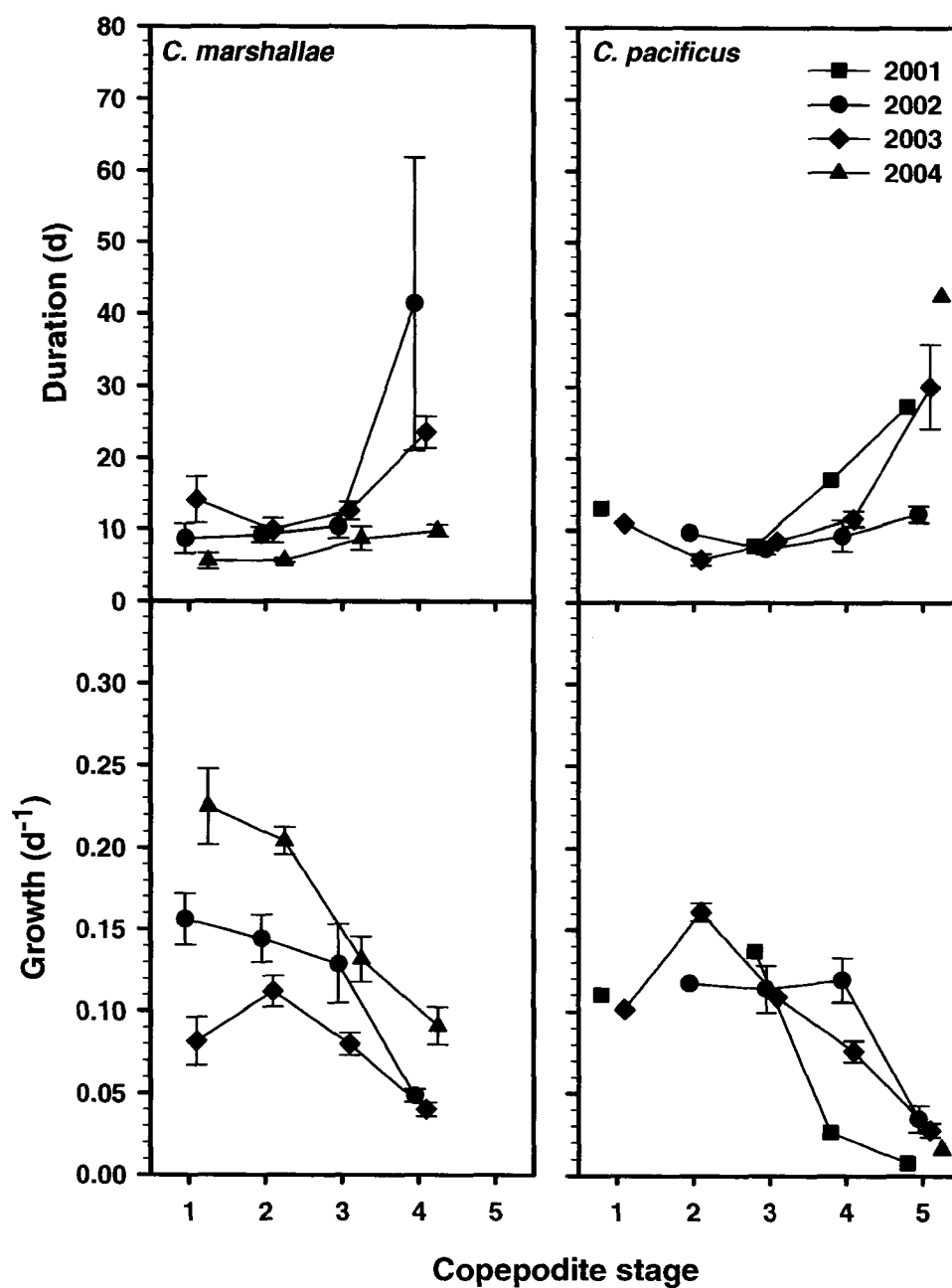
**Figure 3.2** Relationship between prosome length (PL,  $\mu\text{m}$ ) and dry weight (DW,  $\mu\text{g}$ ) for *Calanus marshallae* and *C. pacificus* stages C2–C6 in the northern Gulf of Alaska.



**Figure 3.3** Chlorophyll *a* concentration at study sites averaged over the upper 30 m (bars) and incubation temperatures of experiments at sea in the northern Gulf of Alaska 2001–2004 (circles). Error bars are standard deviations.

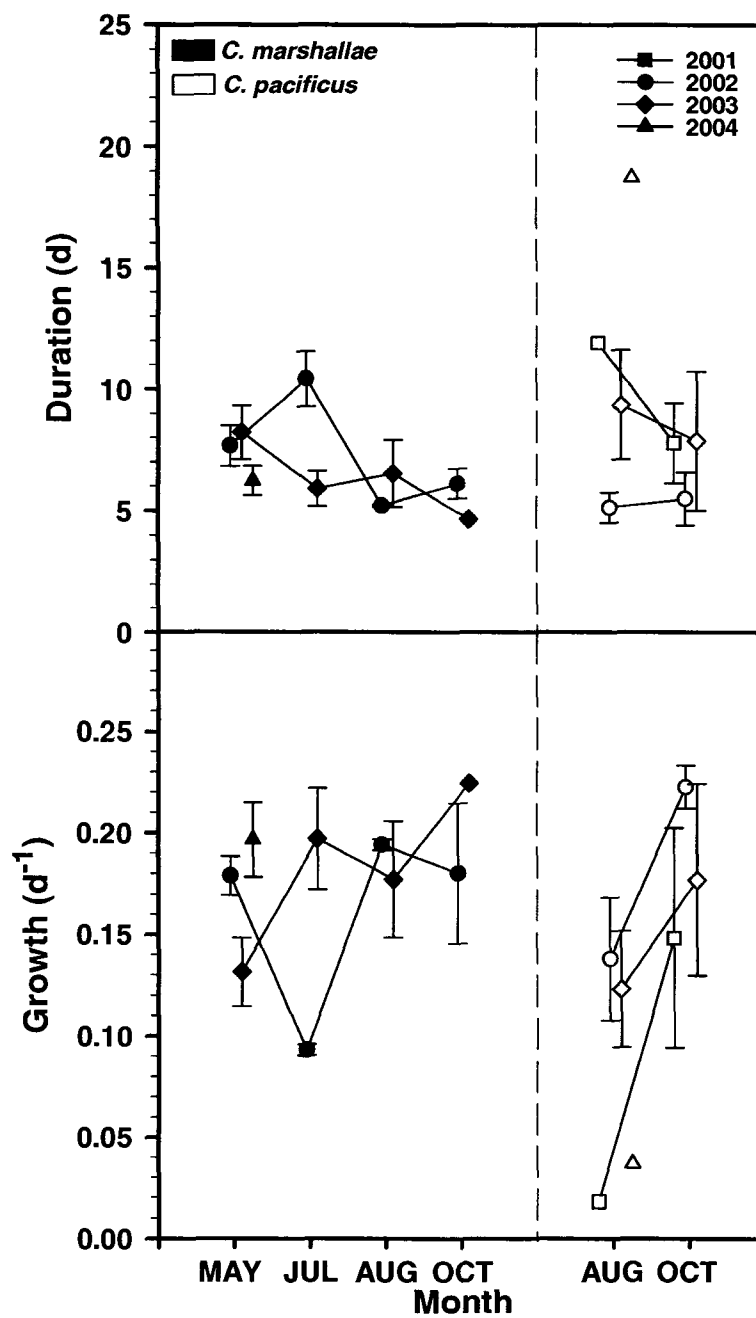


**Figure 3.4** Stage durations (upper panels) and growth rates (lower panels) of *Calanus marshallae* and *C. pacificus* in the northern Gulf of Alaska 2001–2004. Stage is the average of the population at start of incubation.

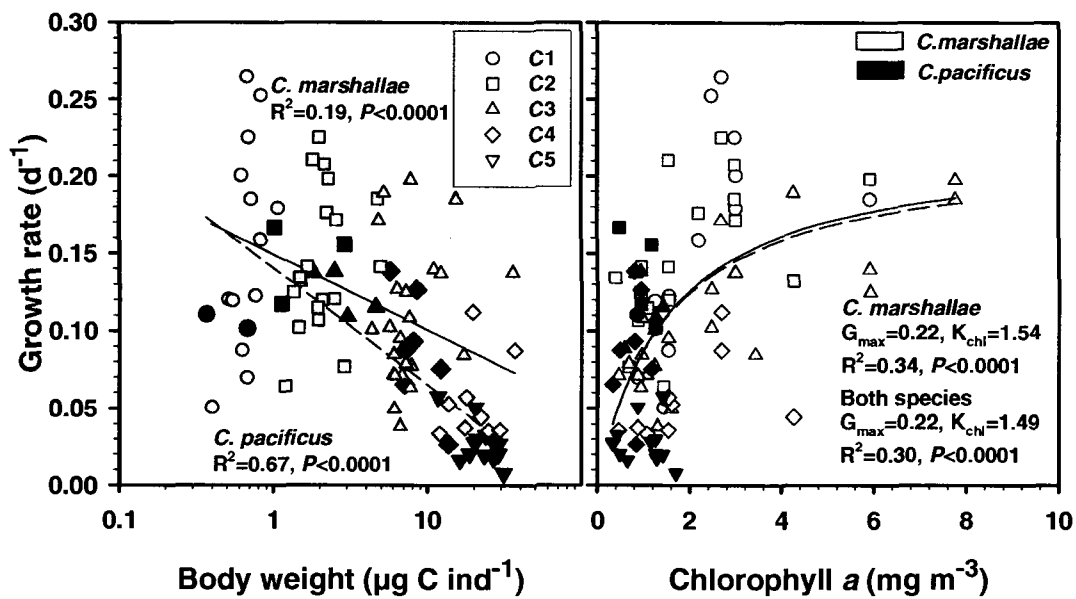


**Figure 3.5** Mean stage duration and growth rate both corrected to 5°C for *Calanus marshallae* and *C. pacificus* in the northern Gulf of Alaska 2001–2004. Values plotted against initial stage and offset to improve interpretation. Error bars are standard errors.

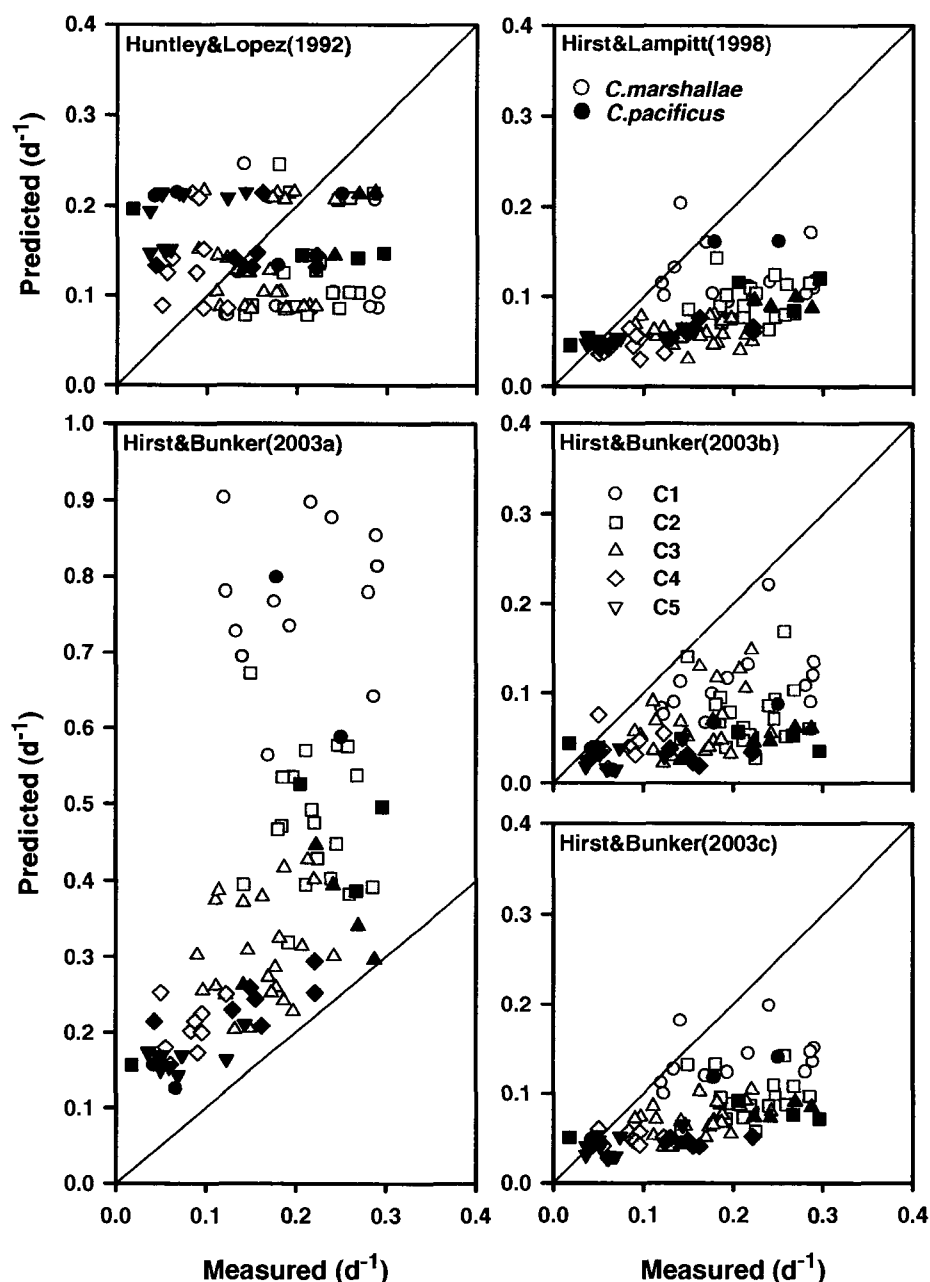




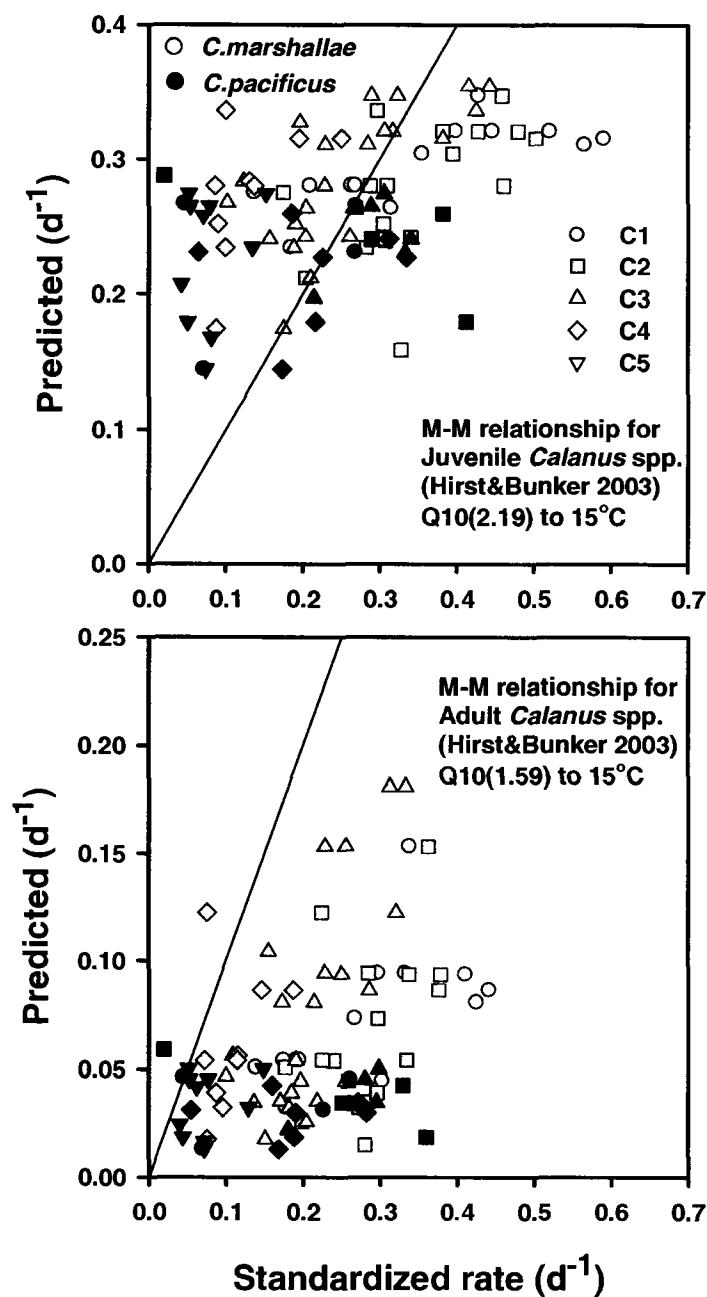
**Figure 3.6** Seasonal mean stage duration and growth rate of *Calanus marshallae* and *C. pacificus* in the northern Gulf of Alaska 2001–2004. Values plotted against initial stage and offset to improve interpretation. Error bars are standard errors.



**Figure 3.7** Relationship between temperature-corrected growth rates and body size, total chlorophyll *a* for *Calanus marshallae* and *C. pacificus* in the northern Gulf of Alaska.



**Figure 3.8** Comparisons of the measured growth rates for *Calanus marshallae* and *C. pacificus*, and growth rates predicted from the models of Huntley and Lopez (1992), Hirst and Lampitt (1998), and Hirst and Bunker (2003). Hirst and Lampitt (1998) equation for all data equation (adults and juveniles of both broadcast and sac-spawners); Hirst and Bunker (2003) a: for juveniles broadcasters; b: for adult broadcasters; c: for all data combined.



**Figure 3.9** Comparisons of the temperature-corrected growth rates for *Calanus marshallae* and *C. pacificus* with the rates predicted from the Michaelis-Menten relationships given for *Calanus* spp. by Hirst and Bunker (2003).

**Table 3.1** Comparison of monthly growth rate ( $\text{day}^{-1}$ ) and development times (days, in parenthesis) based on all observations for *Calanus marshallae* and *C. pacificus* in the northern Gulf of Alaska. (Means $\pm$ Standard error)

Species	Temp (°C)	Growth rate and developmental time				
		May	July	August	October	Average
<i>Calanus marshallae</i>	5.0-15	0.171 $\pm$ 0.009 (8.5 $\pm$ 0.5)	0.174 $\pm$ 10.024 (6.9 $\pm$ 0.9)	0.165 $\pm$ 0.022 (6.2 $\pm$ 1.0)	0.191 $\pm$ 0.027 (5.7 $\pm$ 0.6)	0.175 $\pm$ 0.008 (6.8 $\pm$ 0.4)
<i>Calanus pacificus</i>	10.0- 15.0			0.119 $\pm$ 0.020 (8.2 $\pm$ 1.3)	0.182 $\pm$ 0.026 (7.2 $\pm$ 1.3)	0.151 $\pm$ 0.016 (7.7 $\pm$ 0.9)

**Table 3.2** Comparison of temperature-corrected growth rates ( $\text{day}^{-1}$ ) and development times (days, in parenthesis) for *Calanus marshallae* and *C. pacificus* in the northern Gulf of Alaska. (Means $\pm$ Standard error)

Species	Temp (°C)	Growth rate and developmental time					Average
		C1	C2	C3	C4	C5	
<i>Calanus marshallae</i>	5.0	0.156 $\pm$ 0.019 (9.4 $\pm$ 1.5)	0.145 $\pm$ 0.011 (8.7 $\pm$ 0.8)	0.109 $\pm$ 0.009 (11.0 $\pm$ 0.8)	0.057 $\pm$ 0.008 (18.7 $\pm$ 2.5)		0.117 $\pm$ 0.007 (11.9 $\pm$ 0.7)
<i>Calanus pacificus</i>	5.0	0.106 $\pm$ 0.004 (12.0 $\pm$ 1.0)	0.147 $\pm$ 0.015 (7.2 $\pm$ 1.3)	0.118 $\pm$ 0.009 (7.7 $\pm$ 0.5)	0.088 $\pm$ 0.014 (11.4 $\pm$ 1.4)	0.027 $\pm$ 0.004 (22.0 $\pm$ 3.4)	0.074 $\pm$ 0.009 (15.0 $\pm$ 1.9)

**Table 3.3** Relationship for *Calanus marshallae* between growth rate ( $Gr$ ,  $g\ day^{-1}$ ), initial stage ( $Stg$ ), incubation temperature ( $T$ ,  $^{\circ}C$ ), total chlorophyll  $a$  concentration ( $Chl$ ,  $mg\ m^{-3}$ ), and body size ( $BW$ ,  $\mu g\ C\ individual^{-1}$ ) in the northern Gulf of Alaska

Function	Equation	n	T ( $^{\circ}C$ )	Coefficients ( $p$ )					$r^2(p)$
Multiple Regression	$\log Gr = a_1 + a_2 T + a_3 Chl + a_4 \log BW + a_5 Stg$	67	5.0-15.0	$a_1$ -0.3659 (0.0114)	$a_2$ 0.0228 (0.0038)	$a_3$ 0.0345 (0.0085)	$a_4$ 0.4224 (0.0226)	$a_5$ -0.3891 (0.0003)	0.5943 ( $<0.0001$ )
Michaelis-Menten	$g = Chl[g_{max}]/(Chl + K_{chl})$ (C1-C4)	67	5	$g_{max}$ 0.223 ( $<0.0001$ )			$K_{chl}$ 1.538 (0.0049)		0.337 ( $<0.0001$ )
Michaelis-Menten	$g = Chl[g_{max}]/(Chl + K_{chl})$ (C1-C4)	67	10	$g_{max}$ 0.366 ( $<0.0001$ )			$K_{chl}$ 1.534 (0.0049)		0.337 ( $<0.0001$ )
Composite Nonlinear	$g = a * \log BW + Chl[g_{max}]/(Chl + K_{chl})$ (C1-C4)	67	5	$a$ -0.0476 ( $<0.0001$ )	$g_{max}$ 0.2405 ( $<0.0001$ )		$K_{chl}$ 1.0723 ( $<0.0001$ )		0.546 ( $<0.0001$ )
Composite Nonlinear	$g = a * \log BW + Chl[g_{max}]/(Chl + K_{chl})$ (C1-C4)	67	10	$a$ -0.0782 ( $<0.0001$ )	$g_{max}$ 0.3952 ( $<0.0001$ )		$K_{chl}$ 1.0723 ( $<0.0001$ )		0.546 ( $<0.0001$ )

**Table 3.4** Functional relationships for combined *Calanus marshallae* and *C. pacificus* between growth rate ( $Gr$ ,  $g\ day^{-1}$ ), total chlorophyll  $a$  concentration ( $Chl$ ,  $mg\ m^{-3}$ ), and body size ( $BW$ ,  $\mu g\ C\ individual^{-1}$ ) in the northern Gulf of Alaska

Function	Equation	n	T (°C)	Coefficients ( $p$ )			$r^2(p)$
Michaelis-Menten	$g = Chl[g_{max}]/(Chl + K_{ch})$ (C1–C4)	97	5	$g_{max}$ 0.2182 ( $<0.0001$ )	$K_{chl}$ 1.5563 (0.0049)		0.3038 ( $<0.0001$ )
Michaelis-Menten	$g = Chl[g_{max}]/(Chl + K_{ch})$ (C1–C4)	97	10	$g_{max}$ 0.3585 ( $<0.0001$ )	$K_{chl}$ 1.5563 (0.0049)		0.3038 ( $<0.0001$ )
Composite Nonlinear	$g = a * \log BW + Chl[g_{max}]/(Chl + K_{ch})$ (C1–C4)	97	5	$a$ -0.0529 ( $<0.0001$ )	$g_{max}$ 0.2169 ( $<0.0001$ )	$K_{chl}$ 0.7101 ( $<0.0001$ )	0.554 ( $<0.0001$ )
Composite Nonlinear	$g = a * \log BW + Chl[g_{max}]/(Chl + K_{ch})$ (C1–C4)	97	10	$a$ -0.087 ( $<0.0001$ )	$g_{max}$ 0.3563 ( $<0.0001$ )	$K_{chl}$ 0.7101 ( $<0.0001$ )	0.554 ( $<0.0001$ )



**Table 3.5** Comparison of growth rates ( $\text{day}^{-1}$ ) and development times (days, in parenthesis) for *Calanus marshallae* in the subarctic Pacific and Oregon coast. Daily specific egg production (SEP,  $\text{day}^{-1}$ ) of females included for comparison. (Means $\pm$ Standard error)

Location	Temp (°C)	Growth rate and developmental time							Source
		C1	C2	C3	C4	C5	SEP	Average	
Gulf of Alaska	10	0.257 $\pm$ 0.031 (5.7 $\pm$ 0.9)	0.238 $\pm$ 0.017 (5.3 $\pm$ 0.5)	0.179 $\pm$ 0.016 (6.7 $\pm$ 0.5)	0.094 $\pm$ 0.014 (14.0 $\pm$ 2.9)		0.10*	0.192 $\pm$ 0.012 (7.9 $\pm$ 0.6)	This study
Southeastern Bering Sea	0.5-6.0	0.15 (6.5)	0.15 (6.5)	0.14 (8)			0.06	0.147 (7)	Vidal and Smith(1986)
Oregon coast	11.8		0.19 (3.8)	0.20 (3.7)	0.14 (5.3)	0.12 (5.9)	0.05	0.14 (4.7)	Peterson <i>et al.</i> , (2002)
Oregon coast	10	0.176 (4.3)	0.176 (4.6)	0.176 (6.8)	0.176 (6.2)	0.024 (20.9)		0.146 (8.56)	Peterson (1986)

\* Hopcroft, unpublished data

**Table 3.6** Standardized growth rate ( $\text{day}^{-1}$ ) of *Calanus marshallae* and *C. pacificus* to 5 °C using  $Q_{10}$  (2.7) compared with other dominant species in the northern Gulf of Alaska. Daily specific egg production (SEP,  $\text{day}^{-1}$ ) of females included for comparison. (Means $\pm$ Standard error)

Species	Temp (°C)	Growth rate	SEP	Location	Source
<i>Calanus marshallae</i>	5.0	0.118 (0.007)		Gulf of Alaska	Present study
<i>Calanus pacificus</i>	5.0	0.074 (0.009)		Gulf of Alaska	Present study
<i>Metridia pacifica</i>	5.0	0.083 (0.005)		Gulf of Alaska	Liu and Hopcroft (2006b)
<i>Metridia pacifica</i>	5.0		0.10	Gulf of Alaska	Hopcroft <i>et al</i> (2005)
<i>Metridia okhotensis</i>	5.0		0.11	Gulf of Alaska	Hopcroft <i>et al</i> (2005)
<i>Neocalanus flemingeri/plumchrus</i>	5.0	0.107 (0.005)		Gulf of Alaska	Liu and Hopcroft (2006a)
<i>Centropages abdominalis</i>	5.0	0.141*		Gulf of Alaska	Slater and Hopcroft (2005)

\*Growth rate corrected from original 6.9°C to 5.0°C ( $Q_{10}=2.7$ )

**Table 3.7** Comparison of growth rates predicted by global models with measured rates for *Calanus marshallae* and *C. pacificus* in the northern Gulf of Alaska

<i>C. marshallae</i>		Percent of predicted to rates measured in this study					
Model	Temperature (°C)	C1	C2	C3	C4	C5	C1-C5
Huntley and Lopez (1992)	5.0-15.0	59%	63%	84%*	165%	270%	78%
Hirst and Lampitt (1998)	5.0-15.0	61%	42%	37%	54%	69%*	46%
Hirst and Bunker (2003)a	5.0-15.0	380%	212%	190%	249%	312%	250%
Hirst and Bunker (2003)b	5.0-15.0	56%	33%	42%	53%	58%*	43%
Hirst and Bunker (2003)c	5.0-15.0	68%	41%	44%	58%	67%*	50%
Hirst and Bunker (2003)d	15.0	82%*	79%	112%*	210%	274%	102%*
Hirst and Bunker (2003)e	15.0	26%	21%	37%	57%	67%*	31%

<i>C. pacificus</i>		Percent of predicted to rates measured in this study					
Model	Temperature (°C)	C1	C2	C3	C4	C5	C1-C5
Huntley and Lopez (1992)	10.0-15.0	81%*	56%*	72%*	96%*	310%	122%*
Hirst and Lampitt (1998)	10.0-15.0	75%*	42%	37%	40%	80%*	51%
Hirst and Bunker (2003)a	10.0-15.0	332%*	183%	150%	157%	257%	196%
Hirst and Bunker (2003)b	10.0-15.0	36%*	19%	21%	19%	49%	27%
Hirst and Bunker (2003)c	10.0-15.0	60%*	31%	31%	30%	68%*	41%
Hirst and Bunker (2003)d	15.0	93%*	63%*	82%*	100%*	320%	124%*
Hirst and Bunker (2003)e	15.0	16%	10%	14%	15%	52%	20%

\* non-significant at  $\alpha=0.05$ , two sample, two tail t-Test assuming unequal variance. The apparently large difference for *C. pacificus* C1 is not significant due to limited observations.

In Hirst and Bunker (2003), a: for juvenile broadcasters; b: for adult broadcasters; c: for all data; d: Michaelis-Menten relationship for juvenile *Calanus* spp at 15 °C; e: Michaelis-Menten relationship for adult *Calanus* spp at 15 °C.

***Chapter 4*****Growth and development of *Pseudocalanus* spp. in the northern Gulf of  
Alaska\***

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**ABSTRACT**

*Pseudocalanus* species are the numerically dominant calanoid copepods in coastal subarctic Pacific waters. We examined juvenile growth rates, and explored their relationships to temperature, chlorophyll *a* and body size for *Pseudocalanus* spp. from 2002–2004 in the northern Gulf of Alaska. Generally, the monthly mean growth rates increased from March ( $0.047 \pm 0.009$  (SE)  $\text{day}^{-1}$ ) to August ( $0.076 \pm 0.019$   $\text{day}^{-1}$ ), then declined slightly in October ( $0.064 \pm 0.009$   $\text{day}^{-1}$ ). Typically, growth rates at most stations were around  $0.05$   $\text{day}^{-1}$ , with no consistent or significant pattern between stations. After standardization to  $5^{\circ}\text{C}$  and  $10^{\circ}\text{C}$ , the mean growth rates were  $0.042 \pm 0.003$   $\text{day}^{-1}$  and  $0.068 \pm 0.004$   $\text{day}^{-1}$ , respectively, with growth rate decreasing with increasing development stage. Unlike other local calanoid copepod species, *Pseudocalanus* species tend to be more temperature-dependent than food-dependent, with composite statistical models describing up to 40% of the observed variability in growth rate. Interestingly, although development time was comparable to other co-occurring calanoid copepods, growth rates of *Pseudocalanus* spp. were considerably slower. Thus, the egg-carrying *Pseudocalanus* spp. appear to employ a life history strategy optimized for slow growth at low chlorophyll concentration that also keeps individuals relatively small, and may therefore reduce visual predation upon them.

**Keywords:** Growth, development, functional relationship, *Pseudocalanus* spp., Gulf of Alaska

## INTRODUCTION

Calanoid copepods are the most important metazoan components in the marine pelagic ecosystem, accounting for up to 80% of the metazoan biomass in the marine environment (Verity and Smetacek, 1996). As grazers on both phytoplankton and other protists, and the prey for animals at higher trophic levels copepods play a vital ecological role linking the low trophic levels to higher levels. Our knowledge of their life parameters (e.g. development time, growth rate, and egg production) provides fundamental information on the energy and matter transformation in pelagic food webs. Thus, over the past few decades copepod productivity has become a central aspect of marine plankton research (Poulet *et al.*, 1995; Runge and Roff, 2000). Growth is a key component in determining secondary production and is needed to understand the roles of copepods in the flow of matter and energy in the sea (Kiørboe, 1997).

Although direct estimation of *in situ* somatic growth rates is tedious, the logistically simpler surrogate of “egg production” (e.g. Sekiguchi *et al.*, 1980; Runge and Roff, 2000) does not necessarily reflect juvenile somatic growth (Hopcroft and Roff, 1998; Richardson and Verheye, 1998; Hirst and McKinnon, 2001; Hirst and Bunker, 2003; Hirst *et al.*, 2005). Thus, at present, we know relatively little of the rate of growth by juvenile copepods in nature, and most work has been done in temperate waters at 13–20°C (see Hirst and Bunker, 2003). The lack of data was pronounced for copepod species in the subarctic north Pacific, although recent studies have begun to fill this void for the larger species in this region (Liu and Hopcroft, 2006a, b, in review). The lack of vital rates for small-bodied copepods, such as *Pseudocalanus*, remains a noticeable deficiency.

Copepods of the genus *Pseudocalanus* are small particle-feeding species, which frequently dominate the zooplankton collections in temperate-boreal neritic waters of the northern hemisphere (Corkett and McLaren, 1978). On the Gulf of Alaska shelf, and in the adjacent Bering Sea, *Pseudocalanus* numerically rank as the second most abundant copepods after *Oithona* among the crustacean zooplankton assemblages (Cooney, 1986; Cooney *et al.*, 2001; Incze *et al.*, 1997; Coyle and Pinchuk, 2002, 2003, 2005), are the top

secondary producers (Coyle and Pinchuk, 2003), and are important prey items for both larval and juvenile fish in the northern Gulf of Alaska and the adjacent Bering Sea (Kendall and Nakatani, 1991; Hilgruber *et al.*, 1995, Napp *et al.*, 1996; Schabetsberger *et al.*, 2003). Until recently, *Pseudocalanus* were often considered a species complex, and we now appreciate that at least 7 species coexist in this genus. Two common species (*P. minutus* and *P. newmani*) occur in the temperate-boreal waters of the northwestern Pacific (Frost, 1989). The most recent study reports that *P. mimus*, *P. newmani* and, to a much lesser extent, *P. minutus* are the common species in the coastal Gulf of Alaska (Napp *et al.*, 2005).

Compared to congeneric species in the northern Atlantic Ocean, *Pseudocalanus* species in the subarctic Pacific have received less attention in terms of “growth rates”; *in situ* somatic growth has only been studied once in the southeastern Bering Sea (Vidal and Smith, 1986), laboratory rates examined once for *P. newmani* (Lee *et al.*, 2003), and egg production has been estimated in relatively few field studies (Dagg *et al.*, 1984; Paul *et al.*, 1990; Siefert, 1994; Ban *et al.*, 2000; Napp *et al.*, 2005). Even in more temperate waters, few studies have considered field estimates of somatic growth, although several studies have again considered egg production (Gómez-Gutiérrez and Peterson, 1999; Peterson *et al.*, 2002; Halsband-Lenk *et al.*, 2005). Our best knowledge of *Pseudocalanus* somatic rates still comes from laboratory study (i.e. Vidal, 1980a, b). Despite their importance, our knowledge of *in situ* growth rates of *Pseudocalanus* spp. in the north Pacific remains limited.

This study aims to determine the juvenile growth rates of this ecologically important, small-bodied, and egg-carrying copepod, and explore the fundamental relationships to temperature, food concentrations and body size through a multiple year field study in the northern Gulf of Alaska. As the finale to our studies of copepod growth in this region, we also test the hypothesis that small-bodied copepods grow faster than large ones (e.g. Hopcroft *et al.* 2005; Hirst and Bunker, 2003), and that egg-carrying species may grow more slowly than broadcast spawning species (Hirst and Lampitt, 1998; Hirst and Bunker, 2003).

## METHOD

The sample collections and experiments were conducted during the U.S. Northeast Pacific GLOBEC program in the Coastal Gulf of Alaska (Weingartner *et al.*, 2002). This region is characterized by a shelf of 100–300 m depth, with complex bathymetry and many deep-water coastal fjords and embayments (Fig. 4.1). There were six cruises conducted in March, April, May, June/July, August, and October of 2002 and 2003. Three cruises sailed in March, May and June/July of 2004. Experimental work was set up at four Gulf of Alaska (GAK) stations along the Seward line from inshore to just past the shelf break (i.e. GAK1, 4, 9, 13), plus one station along Knight Island Passage in western Prince William Sound (PWS—either KIP2 or PWS2) where the depth is 500–800 m (Fig. 4.1). Water samples for assessment of ambient phytoplankton concentration at these stations were collected at multiple depths by 5 L Niskin bottles on a CTD rosette, serially size-fractionated using 20  $\mu$ m Poretics, 5  $\mu$ m Nuclepore and GF/F filters, with frozen samples later analyzed fluorometrically for chlorophyll *a* concentration (D. Stockwell and T. Whitledge, unpublished data).

Experimental methodology is identical to that employed successfully for other species in this area (Liu and Hopcroft, 2006a, b, in review). Seawater for incubations at each station was collected by replicate CTD casts with a 12 place rosette of 10 L Niskin bottles equipped with 9 mm valves. Collections were typically made within the upper mixed layer, usually from 5 to 20 m depth, but at inshore (GAK1) and PWS stations, the depths for seawater collection were occasionally deepened to avoid salinities of less than 30 caused by freshwater runoff. Incubation seawater was prescreened through 100  $\mu$ m Nitex mesh sacs placed over the ends of Tygon tubing while draining the bottles into 20 liter soft-walled carboys. Once filled, carboys were stored in large insulated fish tubs ( $\sim 1$  m<sup>3</sup> capacity) rigged as flow through incubators and equipped with a fenestrated lid that reduced lighting to  $\sim 20\%$  of ambient surface illumination. Food concentrations of incubation seawater at the beginning and the end of experiments were measured as size-fractionated chlorophyll *a* using the same protocols and fluorometric techniques employed for monitoring activities.



At each of the experimental stations, copepods were collected using a 64  $\mu\text{m}$  plankton net with 4 L cod-end fished slowly from the surface to 50 m and back to the surface ( $\sim 20 \text{ m}^3$  of water) between 0800 and 1200 hrs. Immediately upon retrieval, copepod collections were diluted using the pre-screened seawater and placed into an incubator at ambient surface water temperatures. Soon after, copepods were sorted into “artificial cohorts” (Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Hopcroft and Roff, 1998; Hopcroft *et al.*, 1998) by sequential passage through submerged screens of the following mesh sizes: 1300, 1000, 800, 600, 500, 400, 300, 200, 150 and 100  $\mu\text{m}$ . The sample was constantly diluted with pre-screened water cooled at ambient seawater temperature, and as each cohort size-class was created, it was placed into an incubator at ambient seawater temperature. Under ideal conditions, this cohort-creating process took 1 hr, and when chains of large filamentous algae were abundant it took up to 3 hours.

Prior to incubation, each size-fraction was gently homogenized and evenly divided. One half was concentrated and preserved in a 5% buffered seawater formalin as the time zero sample (T-0), and the other half equally divided among several of the 20 L carboys previously filled with prescreened seawater. The number of carboys employed varied depending on the biomass of copepods being added. The labeled carboys were put back into the on-deck incubators and maintained at surface water temperatures by running seawater. The temperature variation inside the incubators was recorded by Onset Tidbit loggers. Presumably, the ship movement was sufficient to keep phytoplankton in suspension during the incubation. After 5 days (in March, April and May) and 4 days (in June/July, August and October) the carboys were filtered through 45  $\mu\text{m}$  sieves, copepods were pooled by the original size fractions, and they were preserved immediately in 5% buffered seawater formalin as the final sample (T-5 or T-4). All preserved material was stained with Rose Bengal.

Although it is clear that three species occur in these collections (Napp *et al.*, 2005), laboratory sorting of early copepodites of *Pseudocalanus* proved problematic. Thus, preserved copepodites were only identified to developmental stages and grouped together as *Pseudocalanus* spp. Copepodite prosome lengths were digitally measured (Roff and

Hopcroft, 1986), and the progression of the cohorts was determined by changes in the stage and body size. Copepodite dry weights were predicted from a published length-weight relationship:  $\log_{10}DW = 2.732 \times \log_{10}PL - 6.916$ , where PL (prosoma length) is in  $\mu\text{m}$ , and DW (dry weight) is in  $\mu\text{g}$  (Hay *et al.*, 1991). To convert dry weight (DW) to carbon weights, 40% carbon content in dry weight for copepods is assumed (Båmstedt, 1986).

Development time was calculated as  $1/\text{MR}$ , where MR is the observed molting rate of each cohort. This approach may be subject to some errors (Hirst *et al.*, 2005), because we frequently lacked concurrent site experiment-specific molt rates for adjoining cohort “stages”, and because our experiments typically contain a mixture of multiple stages, the modified molt rate (MMR) method was not employed. The growth rate ( $\text{day}^{-1}$ ) within a given cohort over the incubation time  $t$  (days) was computed from the equation  $g = (\ln W_t - \ln W_0)/t$ , where  $W_0$  and  $W_t$  are the mean dry weight of artificial cohorts at the start and the end of incubation period  $t$  (days) (Runge and Roff, 2000). Recent concerns over growth rate errors using the molt rate method (Hirst *et al.*, 2005) are not operational in this study, because we employ incubation periods not development time to estimate our growth rates. Some bias and “noise” may exist in our estimates because we have used weight predicted from length-weight analysis rather than direct measurements of weights (Kimmerer *et al.*, in press), and this is unavoidable by our methods.

Multiple regression analysis of the relative effects of developmental stage, body weight, temperature, chlorophyll *a* concentration and their interactive influences on growth rates of *Pseudocalanus* spp. was conducted (SAS system V9). A composite nonlinear model for *Pseudocalanus* spp. was developed by combined features of SAS (V8) and R (2.2.1) with equivalent  $r^2$  calculated from appropriate model sum of squares (Anderson-Sprecher, 1994). For ease of comparison, growth rates were standardized to 5°C and 10°C using  $Q_{10}$  of 2.7 for juvenile sac spawners (Hirst and Bunker, 2003). For other analyses and all figure-making we used Sigmaplot (V9).

## RESULTS

### Background of environmental conditions

Typically, there is a seasonal signal in incubation temperature in this study area (Liu and Hopcroft, 2006b). Temperatures start warming from 4~5°C in the early spring to 6~7°C in late spring, and peak at ~14°C in late summer before decreasing to ~10°C in fall (Fig. 4.2). This pattern is similar to the variability in water temperature within the upper mixed layer (see Coyle and Pinchuk, 2005); while within each cruise the temperature differences between stations were insignificant (Fig. 4.2). The relatively high temperatures in 2003 were due to an atypically late cruise in May of 2003, and the abnormally warm sea water temperatures of that year.

Seasonal variability of total chlorophyll *a* concentration within the upper 30 m mixed layer was quite similar to the pattern of temperature (Fig. 4.2). Typically, chlorophyll *a* concentration increased from March to April, then peaked in May in reflection of the progression in the spring bloom. After that, it declined from July to October, but still remained relatively high (~1 mg m<sup>-3</sup>) and uniform across sampling stations (Fig. 4.2). The total amount of chlorophyll *a* measured within incubation experiments and present in the upper 30 m mixed layer at the time of collection was not significantly different (paired *t*-test,  $\alpha=0.05$ ), except during the spring bloom when large diatoms were removed by the pre-screening process. The seasonal partitioning of size-fractionated chlorophyll *a* concentration within the prescreened seawater was variable. The larger particle chlorophyll *a* (>20  $\mu$ m) averaged 41–46% of the total during the spring bloom (April and May), and around 20% at other times; the ~0.5–5  $\mu$ m fraction accounted for 25–35% of the total chlorophyll *a* concentrations within the spring bloom, and a relatively high percentage (50–60%) during summer and fall; the medium size chlorophyll *a* (5  $\mu$ m) averaged 20–30% throughout the whole sampling season.

### Growth rate and development time

All stages of *Pseudocalanus* species occurred year-around (Fig. 4.3), suggesting multiple generations annually. Seasonally, the monthly mean growth rates of *Pseudocalanus* spp.

increased from March to August, then declined slightly in October, while the monthly mean development time followed a reciprocal trend. Monthly variability in growth rate and development time between stations or between years was insignificant (Fig. 4.4). Average growth rate and development time across developmental stages can be affected by C5s because of their slow somatic growth, and it is clear that the inclusion of copepodite stage C5 can weaken the overall patterns (Fig. 4.4). Generally, copepodite growth and development (C2–C5) in the spring (March to May) were faster in 2003 than in 2002. The slowest growth rate (with corresponding stage duration in parenthesis) was  $\sim 0.02 \text{ day}^{-1}$  ( $\sim 22$  days) and occurred in March of 2002. The fastest spring rates of  $0.079 \text{ day}^{-1}$  ( $\sim 8.5$  days) and  $0.062 \text{ day}^{-1}$  ( $\sim 15.3$  days) appeared in April and May of 2004, respectively, and are likely due to the favorable conditions caused by the later than typical cruise dates. After peaking in summer (July or August), the growth rates slowed in October. During the summer and fall, the fastest growth and development for C2–C4 was  $0.106 \text{ day}^{-1}$  ( $\sim 3.6$  days) in July 2002, while the slowest (including C2–C5) was  $0.049 \text{ day}^{-1}$  ( $\sim 29$  days) in the same month of 2004. The overall mean of growth rates and development times varied temporally (Fig. 4.4, Table 4.1).

There was no consistent spatial variability in growth rate and development time during each study year after standardization to  $5^{\circ}\text{C}$  ( $Q_{10}$  of 2.7), and this is clear when the slow-growing C5s that contribute variably to samples are excluded (Fig. 4.5). Typically, at most stations growth rates were around  $0.05 \text{ day}^{-1}$  with development times from 9 to 15 days. The annual variability in growth rate at each station was insignificant except for station PWS2 in 2003 (Fig. 4.5). Although the mean growth rates at all sampling stations varied (Table 4.1), differences were not significant (one-way ANOVA,  $P=0.097$ ). After standardization to  $5^{\circ}\text{C}$  and  $10^{\circ}\text{C}$ , the overall mean growth rates and development times were  $0.042 \pm 0.003 \text{ day}^{-1}$  and 16.5 days at  $5^{\circ}\text{C}$ , and  $0.068 \pm 0.004 \text{ day}^{-1}$  and 10.1 days at  $10^{\circ}\text{C}$ , respectively, and exhibited a clear trend of declining growth and development with the development stage (Table 4.2).

### Effects of temperature

Overall, the effect of temperature on growth rates of *Pseudocalanus* spp. was positively significant ( $r^2=0.04$ ,  $P=0.045$ ), while similar analyses for each individual stage were positive for C2 ( $r^2=0.34$ ,  $P=0.003$ ) and C3 ( $r^2=0.23$ ,  $P=0.013$ ), but nonsignificant for C4 ( $r^2=0.017$ ,  $P=0.45$ ) and C5 ( $r^2=0.205$ ,  $P=0.14$ ). The overall relationship between body weight and temperature was negative ( $r^2=0.07$ ,  $P=0.011$ ) (Fig. 4.6), but the only significant relationship for an individual stage was for C4 ( $r^2=0.26$ ,  $P=0.002$ ).

### Functional relationships to growth rate

A significant multiple regression model for growth rates of *Pseudocalanus* spp. ( $r^2=0.333$ ,  $P<0.0001$ ) included developmental stage (partial  $r^2=0.2354$ ), temperature (partial  $r^2=0.0435$ ) and body weight (partial  $r^2=0.0558$ ) as explanatory variables, but there was no relationship to either total chlorophyll *a* or sized-fractionated chlorophyll *a*  $>5\ \mu\text{m}$  (Table 4.3). After standardization to  $5^\circ\text{C}$ , growth rate was negatively correlated to body size for C2–C5 ( $r^2=0.04$ ,  $P=0.046$ ). Within each stage, growth rates appeared positively related to body size (Fig. 4.7); however, the positive relationship between growth rate and body size was only statistically significant for C2 ( $r^2=0.17$ ,  $P=0.047$ ) and C3 ( $r^2=0.16$ ,  $P=0.04$ ), and not for C4 and C5.

The growth rates standardized to  $5^\circ\text{C}$  and  $10^\circ\text{C}$  were not correlated to the total ambient chlorophyll *a* concentration in a typical Michaelis-Menten relationship ( $r^2=0.014$ ,  $P=0.246$ ; Fig. 4.7, Table 4.3). However, such a relationship emerged when chlorophyll was restricted to particles  $>5\ \mu\text{m}$ , for which  $G_{\text{max}}$  and  $K_{\text{chl}}$  were  $0.048\ \text{day}^{-1}$  and  $0.05\ \text{mg m}^{-3}$  at  $5^\circ\text{C}$ , and  $0.079\ \text{day}^{-1}$  and  $0.05\ \text{mg m}^{-3}$  at  $10^\circ\text{C}$  (Table 4.3).

A composite nonlinear model incorporating body size into the classical Michaelis-Menten model indicated body size was negatively related to growth rate, with  $G_{\text{max}}$  and  $K_{\text{chl}}$  ( $>5\ \mu\text{m}$ ) of  $0.067\ \text{day}^{-1}$  and  $0.074\ \text{mg m}^{-3}$  at  $5^\circ\text{C}$ , and  $0.11\ \text{day}^{-1}$  and  $0.074\ \text{mg m}^{-3}$  at  $10^\circ\text{C}$ . In comparison to the Michaelis-Menten model, saturated growth rates of the new model were higher under the high food conditions, and more variability (12–19%) was explained by the composite nonlinear models (Table 4.3). Incorporation of developmental

stage further improved both chlorophyll models, explaining 38–40% of the variation, and notably contained negative relationships to stage, positive relationships to body size, and no significant relationships to chlorophyll.

## DISCUSSION

### **Growth rates of *Pseudocalanus* spp.**

The overall patterns of growth rate are generally consistent with patterns demonstrated elsewhere (e.g. Hirst and Bunker, 2003), and locally for other species (Liu and Hopcroft, 2006a, b, in review). However, estimated growth rates in this study ( $0.02\text{--}0.11\text{ day}^{-1}$  with a mean of  $0.057\text{ day}^{-1}$ ) were low compared to other estimated rates for *Pseudocalanus* in the subarctic Pacific, e.g.  $0.13\text{ day}^{-1}$  measured in the southeastern Bering Sea at temperatures ranging from  $0.5$  to  $6^{\circ}\text{C}$  during high chlorophyll concentrations (Vidal and Smith, 1986), and  $0.22\text{ day}^{-1}$  at  $11.8^{\circ}\text{C}$  measured off the Oregon coast during coastal upwelling (Peterson *et al.*, 2002). Both of these studies appear to have occurred under conditions favorable for growth of copepods, in contrast to the seasonally variable conditions in this study, and likely represent the upper limit of growth rates in the field. Estimates in this study may reasonably represent more typical levels, under conditions of food-limitation. Females typically experience slower growth than copepodites due to food limitation (e.g. Hopcroft and Roff, 1998; Hirst and Bunker, 2003), and that may explain why our estimated juvenile growth rate (corrected to  $10^{\circ}\text{C}$ ) of  $0.066\text{ day}^{-1}$  was consistent with the egg production rate of  $0.06\text{ day}^{-1}$  off the Oregon coast (Peterson *et al.*, 2002).

Globally, developmental rates are similar for egg-carrying and broadcast-spawning copepods (Peterson, 2001). It is notable that the stage durations of *Pseudocalanus* spp. were not significantly different from the corresponding stages of the other four common calanoid species in this area (Fig. 4.8), although growth rates of *Pseudocalanus* spp. were significantly lower (Table 4.4). It seems almost paradoxical that despite annually high abundance and biomass in this area (Coyle and Pinchuk, 2003, 2005), *Pseudocalanus* grows slowly. The numerical dominance of *Pseudocalanus* must, therefore, arise because

it is either more efficient at utilizing resources, has higher fecundity, or experiences lower mortality than other co-occurring species (i.e. *Neocalanus flemingeri/plumchrus*, *Metridia pacifica*, *Calanus marshallae*, *C. pacificus*). All of these other species grow fast (Liu and Hopcroft, 2006a, b, in review), in part because of their relatively short optimal growth season during spring in this area. Although overall egg production rates (i.e. eggs female<sup>-1</sup> day<sup>-1</sup>) in *Pseudocalanus* may be lower than other species of similar size, weight specific egg production rates of this species is comparable to that of local broadcast spawning species (Napp *et al.* 2005, Hopcroft *et al.*, in prep), suggesting a potential for similar growth efficiency. Limited data on mortality in copepods makes determination of underlying patterns difficult, but it appears the mortality of eggs in egg-carrying copepods may be low compared to broadcast species, while overall post-hatch mortality is similar (Hirst and Kiørboe, 2002), suggesting overall survivorship should be better for sac-spawners than broadcast spawners. Egg-carrying cyclopoid females may have a higher mortality than broadcast spawning calanoid species (of similar size) due to a higher susceptibility to their visual predators (Kiørboe and Sabatini, 1994), but in general should be less apparent to visual predators because of their small size. It remains unclear to what extent size may form a refugium from predation in copepods (Hirst and Kiørboe, 2002), but we speculate that *Pseudocalanus* spp. employs slow somatic growth to stay small, thereby minimizing visual predation while carrying sacs. At the the same time it has per capita recruitment to copepodites (and ultimately adults) similar, if not superior, to the other co-occurring calanoids. Further observations on the life history strategy trade-offs of egg-carrying and small-bodied copepods are needed to explore such possibilities.

### **Effects of temperature on growth rates**

Temperature strongly regulates rates of copepod growth (McLaren, 1978; Huntley and Lopez, 1992). Globally, juvenile growth rates are more temperature-dependent for egg-carrying copepods than for broadcasters (Hirst and Lampitt, 1998; Hirst and Bunker, 2003), but temperature-dependent growth rates are invariably confounded with food concentrations and body sizes (Vidal, 1980a; Hirst and Bunker, 2003; Liu and Hopcroft,

2006b). Secondary production by *Pseudocalanus* spp. appears to be controlled more by temperature than by food (McLaren, 1978; Davis 1984; Frost, 1985). In this study, growth rates of *Pseudocalanus* showed a significantly positive relationship to temperature for the group of combined stages C2–C5, as well as for the individual stages C2 and C3. Temperature was also statistically significant in the selected multiple linear regression model (Table 4.3). Moreover, in this study, body sizes of *Pseudocalanus* spp. tended to be negatively related to temperature across stages.

Previous studies reported that *Pseudocalanus* species exhibit large seasonal variability in body length, even within the same species (Yamaguchi *et al.*, 1998; Napp *et al.*, 2005; Renz and Hirche, 2006). Moreover, both higher temperature and lower phytoplankton concentrations are major parameters causing smaller size in adult copepods (McLaren, 1974; Corkett and McLaren, 1978; Vidal, 1980a). Thus, the trend of temperature-dependent body size was largely caused by variable conditions in the Gulf of Alaska, in particular the relatively high temperature in conjunction with low chlorophyll *a* concentrations during summer.

### **Chlorophyll *a*, body size and growth rates**

Standardizing growth rates to a fixed temperature often permit discerning the underlying relationship between growth rates and other factors (i.e. food concentration and body size). Unsurprisingly, standardized rates were negatively related to body size, e.g., the severity of food-limited growth increases with body size (Vidal, 1980a; McKinnon, 1996; Hopcroft *et al.*, 1998; Hirst and Bunker, 2003). However, at each stage, growth rates and body size tend to be positively correlated (Fig. 4.7). This is because under favorable food conditions, animals growing fast tend to be larger than animals growing more slowly (Liu and Hopcroft, 2006a). The relationships were significant for C2 and C3, but not for C4 and C5, which suggests that the younger stages were more optimally fed than later stages. Similar patterns of copepod growth rates and body size were observed for other large calanoid copepods in this area (Liu and Hopcroft, 2006a, b, in review). However, the absence of single stages in our artificial cohort experiments blurs this pattern (Liu and



Hopcroft, 2006b, in review). Based on our studies, it is reasonable to postulate that this pattern exists for all marine copepods.

Standardized growth rates showed significant Michaelis-Menten relationships with chlorophyll *a* concentration ( $>5 \mu\text{m}$ ); however, the variability in growth rates explained by chlorophyll *a* ( $>5 \mu\text{m}$ ) was low (Table 4.3). In fact, chlorophyll *a* concentration was not selected as a significant determinant of growth in the multiple regression analysis. This appears to be the case for egg-carrying copepod species in general (Hirst and Bunker, 2003). Despite growth of egg-carrying being more temperature- than food-dependent, feeding habits and food items of *Pseudocalanus* spp. also need be considered. Originally, *Pseudocalanus* spp. was believed to be primarily herbivorous (Corkett and McLaren, 1978), but more recent studies show that diatoms, flagellates, dinoflagellates, ciliates, heterogeneous particulate matter and even sinking particles could be a food source for *Pseudocalanus acuspes* in the central Baltic Sea (Peter *et al.*, 2006; Renz and Hirche, 2006). Clearly, not all food particles mentioned above contain chlorophyll *a*. Although chlorophyll *a* is the most common indicator of food conditions for aquatic herbivores, it is often an inadequate estimate of actual food availability (Hirst and Bunker, 2003), because of the diversity of the copepod diet. Moreover, laboratory observations suggest that toxins found in some diatom species are harmful for egg viability in copepods (Ianora *et al.*, 2003), although field studies have produced seemingly paradoxical results of either an effect (Miralto *et al.*, 1999) or no effect (Irigoien *et al.*, 2000; Irigoien *et al.*, 2002). *Pseudocalanus* reproduction specifically does have the potential to be impacted by diatom diets (Halsbank-Lenk, *et al.* 2005).

### **Global models**

Given the difficulty in obtaining measurement of somatic growth rates, global growth models have become increasingly appealing in the study of copepod growth and production (i.e. Huntley and Lopez, 1992; Hirst and Lampitt, 1998; Hirst and Bunker, 2003; Bunker and Hirst, 2004). Clearly, global growth models are limited in their predictive capability for any given species in a specific ecosystem, and minor

discrepancies and even large errors can occur when global models are tested under specific conditions (Richardson *et al.*, 2001; Peterson *et al.*, 2002; Rey-Rassat *et al.*, 2004). In our recent studies, global models of copepod growth rates were exhaustively tested for the dominant species in this area (Liu and Hopcroft, 2006a, b, in review), and can now be considered for the small body-sized and egg-carrying *Pseudocalanus* species. Generally, global models provide a reasonable match to directly measured rates for *Pseudocalanus* spp., except for large errors occurring for animals at stage C5 (Fig. 4.9, 4.10; Table 4.5). The obvious overestimation by the simple temperature-dependent model of Huntley and Lopez (Huntley and Lopez, 1992) is due to the implicit assumption that food is not limiting. The general models of Hirst and Bunker (2003) (juvenile sac spawners and for all data; Fig. 4.8) matched well with the directly measured rates, while the model for adult sac spawners (Hirst and Bunker, 2003) underestimated juvenile growth. The three classical Michaelis-Menten models in Hirst and Bunker (2003), including a model for adult *Pseudocalanus* specifically, matched our measured rates for early stages, but errors tended to be large for later stages (Fig. 4.10, Table 4.5). The lack of body size as a parameter in the Hirst and Bunker (2003) Michaelis-Menten models is likely to account for these discrepancies, and further refinement of their models is required.

“Global” models shortcut the complexities and uncertainties found in the experimental studies and use only a few easily measured variables (i.e. temperature, chlorophyll *a* and body size). Confounding effects of temperature, food source and body size on the growth of marine copepods (Vidal, 1980a; Hopcroft *et al.*, 1998; Hirst and Bunker, 2003; Liu and Hopcroft, 2006b, in review) are not addressed. To illustrate these synergistic effects on growth rates, we developed a composite nonlinear model (Liu and Hopcroft, 2006b). This model exhibited higher explanatory power for variability in growth rates of *Pseudocalanus* spp. by including both chlorophyll *a* and body size, rather than just chlorophyll *a* (Table 4.3), and was consistent with results for other copepod species in this area (Liu and Hopcroft, 2006b, in review). In this study, the further addition of stage to the composite model had a profound impact on the utility of the model. In this 4

parameter model, the stage now takes the negative slope we observed in univariate analysis, and the sign of the body-weight parameter changes from the negative “across-stage” pattern to encompass the positive “within-stage” relationship suggested here, as well as for other local species (Liu and Hopcroft, 2006a, b, in review). The 4 parameter model also illustrates the poor utility of chlorophyll *a* in describing growth rate for *Pseudoacalanus*, in contrast to the other broadcast spawning local species (*ibid*; Slater and Hopcroft, 2005).

Thus far, the 3 parameter composite model shows great promise for describing the growth rates of each of the dominant copepods in this ecosystem (Fig. 4.11, Table 4.6). The model shows that although broadcast spawning species have comparable growth rates, the egg-carrying *Pseudocalanus* clearly has lower somatic growth. The latter conclusion is consistent with the generalization from global growth rate syntheses that broadcaster-spawners and egg-carriers differ notably in their rates of somatic growth (Hirst and Lampitt, 1998; Hirst and Bunker, 2003). We suggest that further refinement of global models that incorporation of non-linear relationships, such as utilized in the composite model, and fuller appreciation of the biases inherent in growth rate estimates (Hirst *et al.*, 2005; Kimmerer *et al.*, in press) are required to improve the global models.

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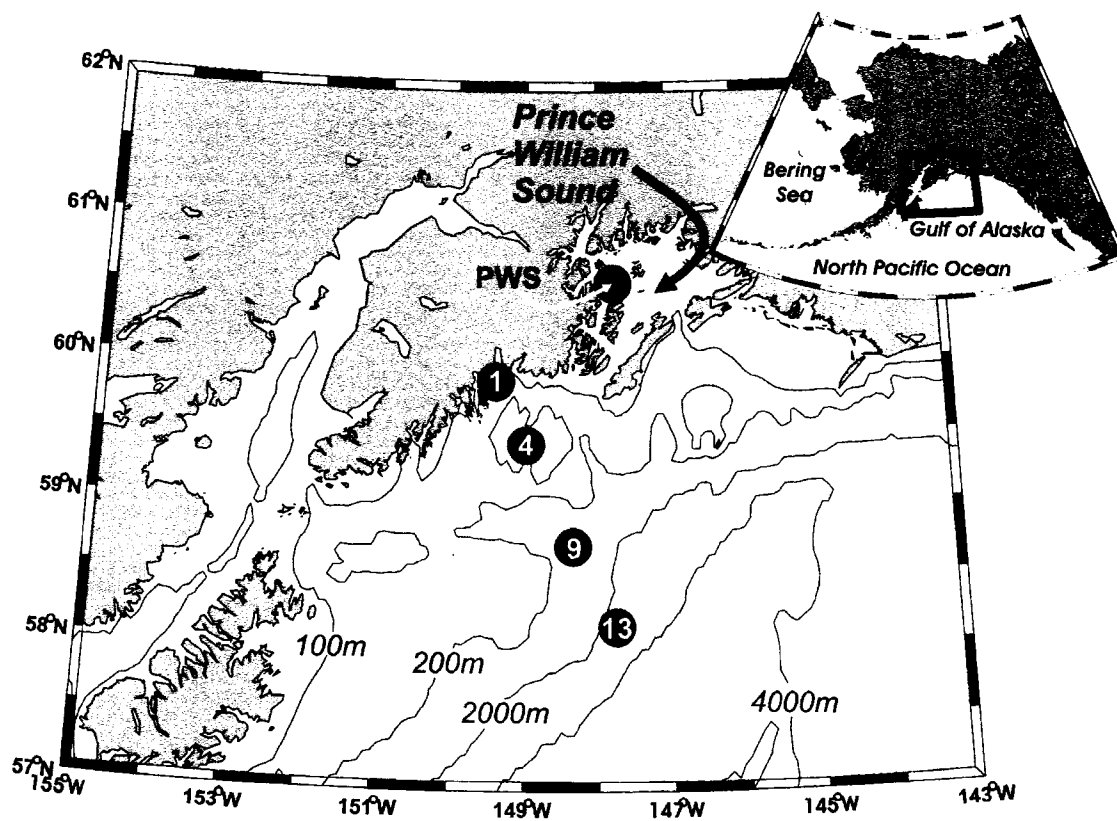
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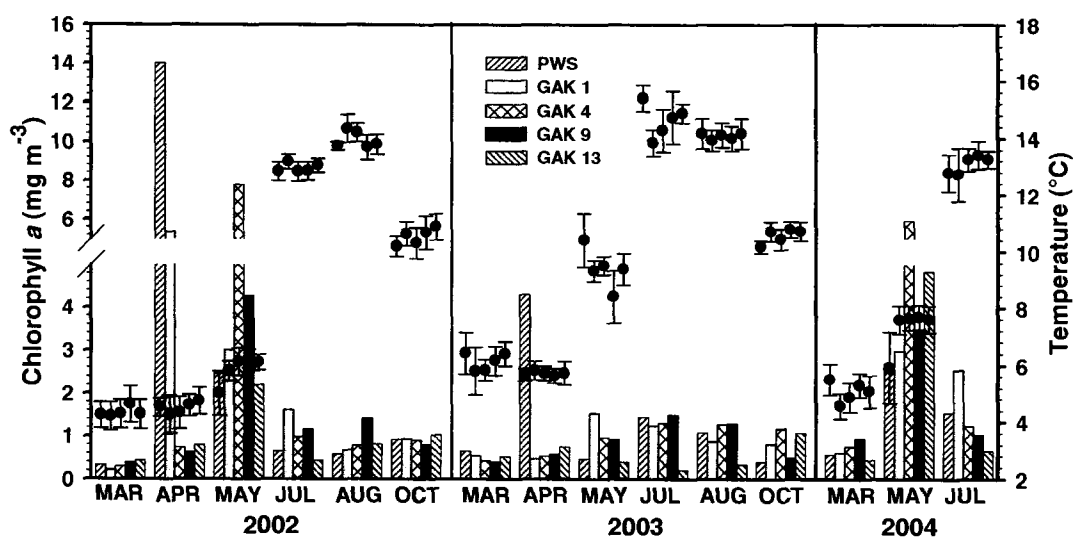


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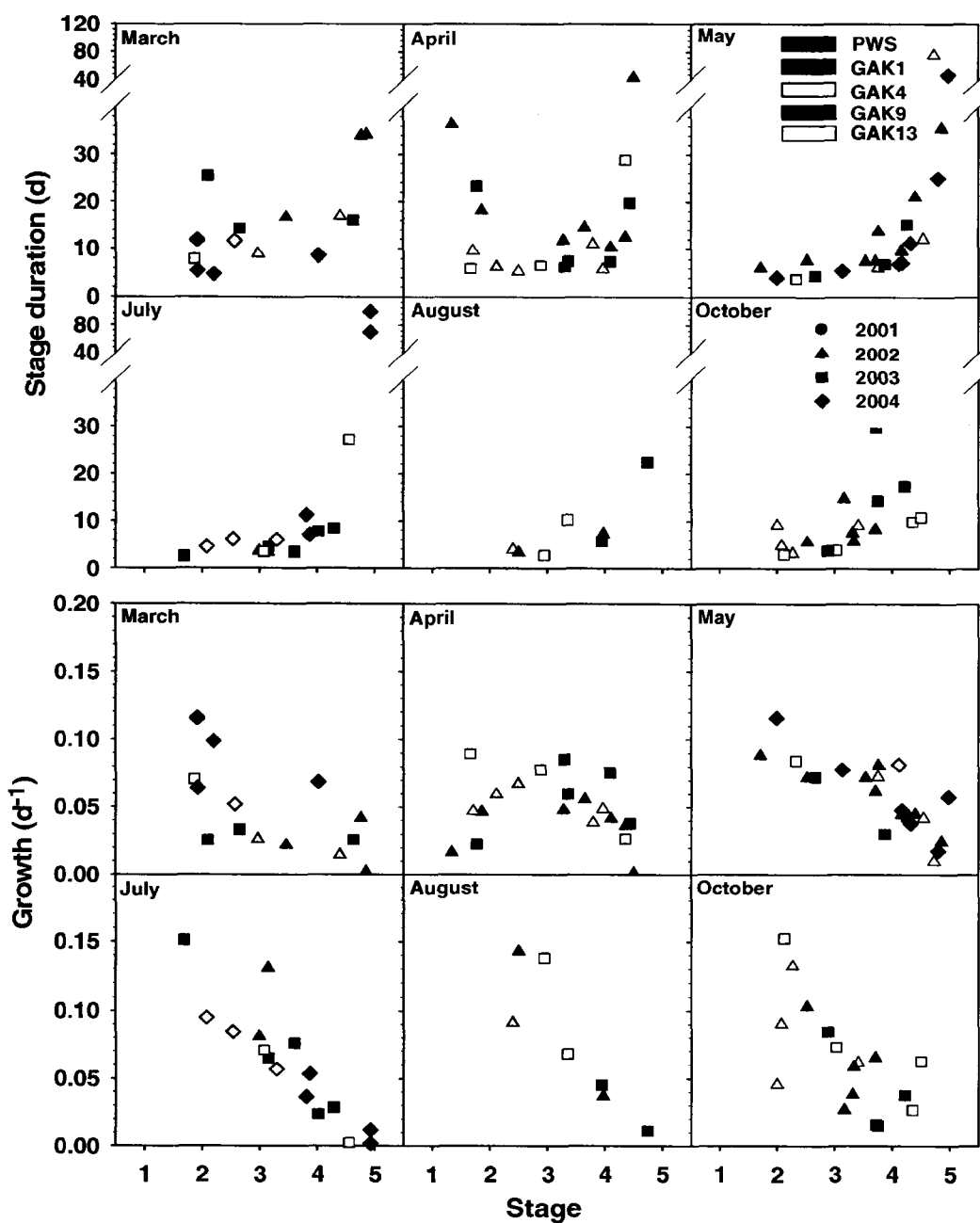
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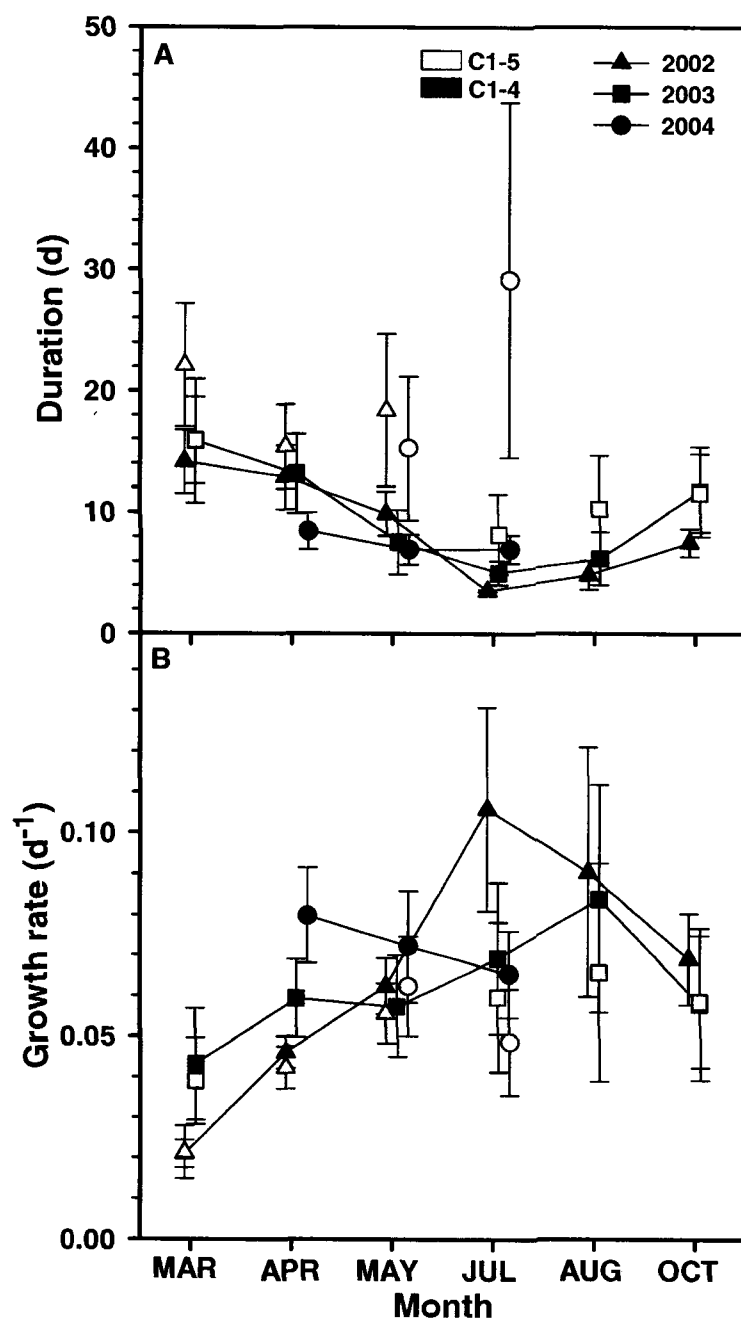
**Figure 4.1** Map of the sampling area in the northern Gulf of Alaska.



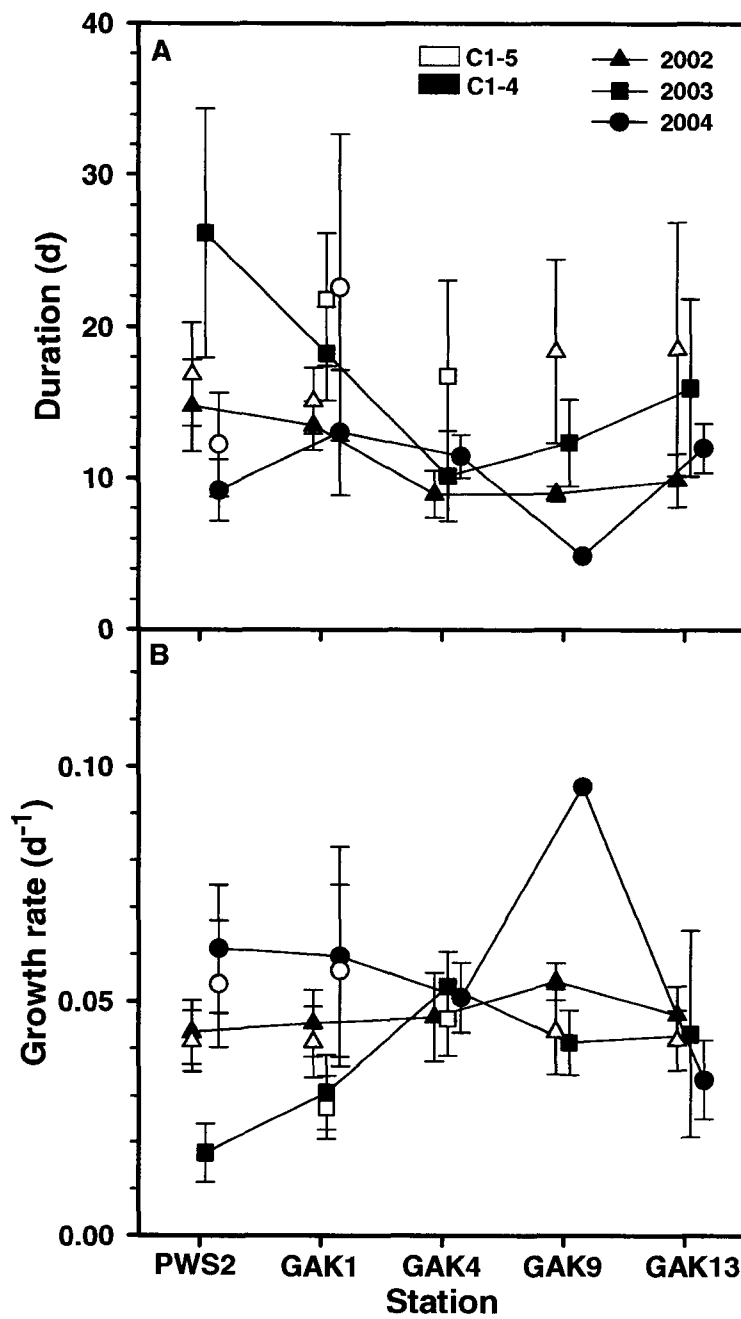
**Figure 4.2** Chlorophyll *a* concentrations at study sites averaged over the upper 30 m (bars) and incubation temperatures of experiments at sea in the northern Gulf of Alaska 2002–2004 (circles). Error bars are standard deviations.



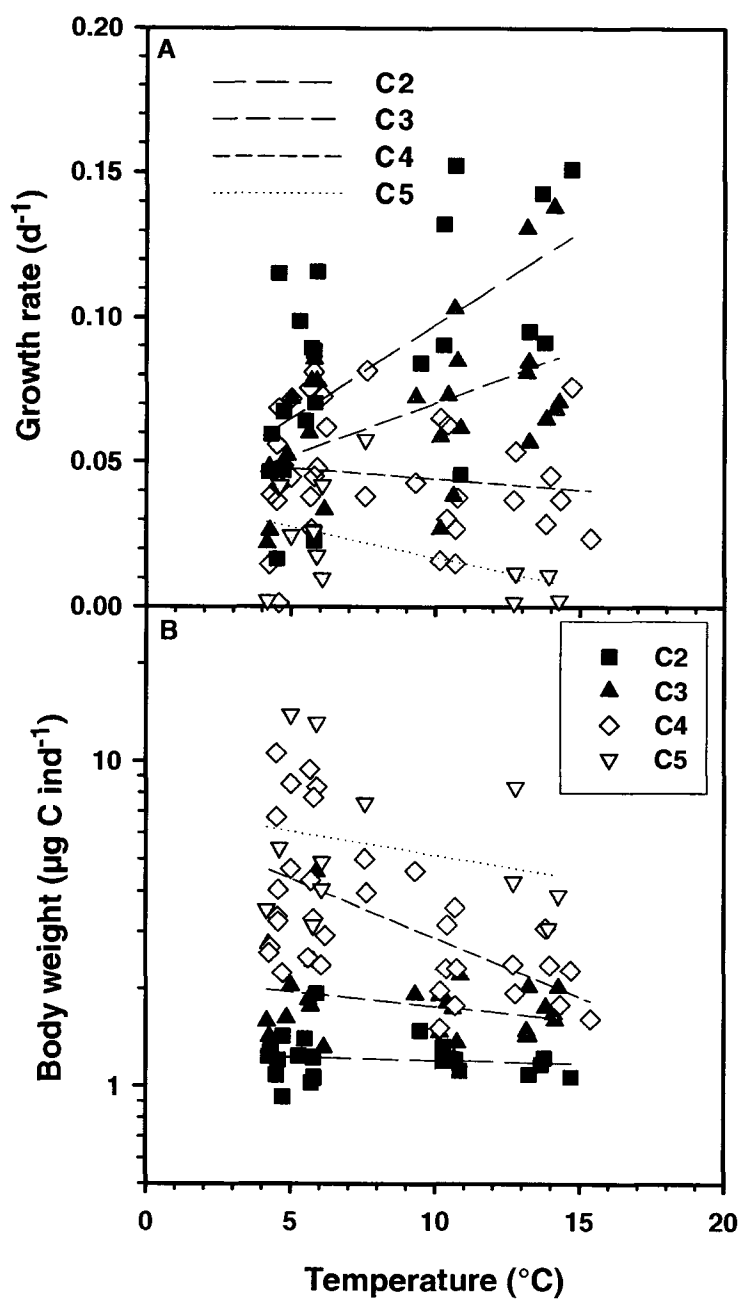
**Figure 4.3** Growth rates and development time of *Pseudocalanus* spp. in the northern Gulf of Alaska 2002–2004. Stage is the average of the population at start of incubation.



**Figure 4.4** Seasonal variability in growth rate and development time of *Pseudocalanus* spp. in the northern Gulf of Alaska 2002–2004.

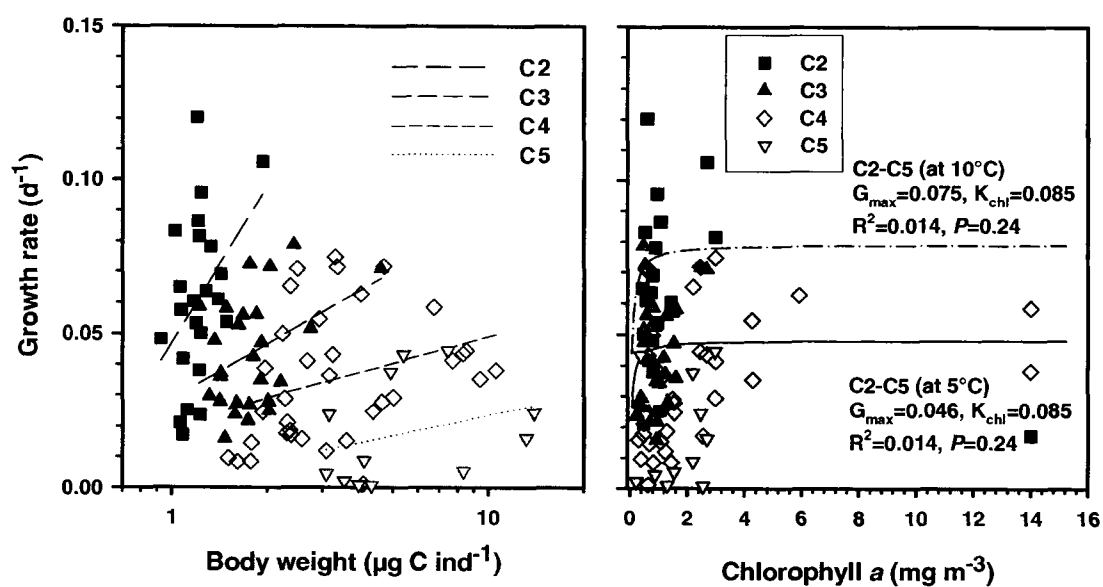


**Figure 4.5** Spatial patterns in growth rate and development time of *Pseudocalanus* spp. in the northern Gulf of Alaska 2002–2004. Data were corrected to 5°C ( $Q_{10}=2.7$ ). Error bars are standard errors.

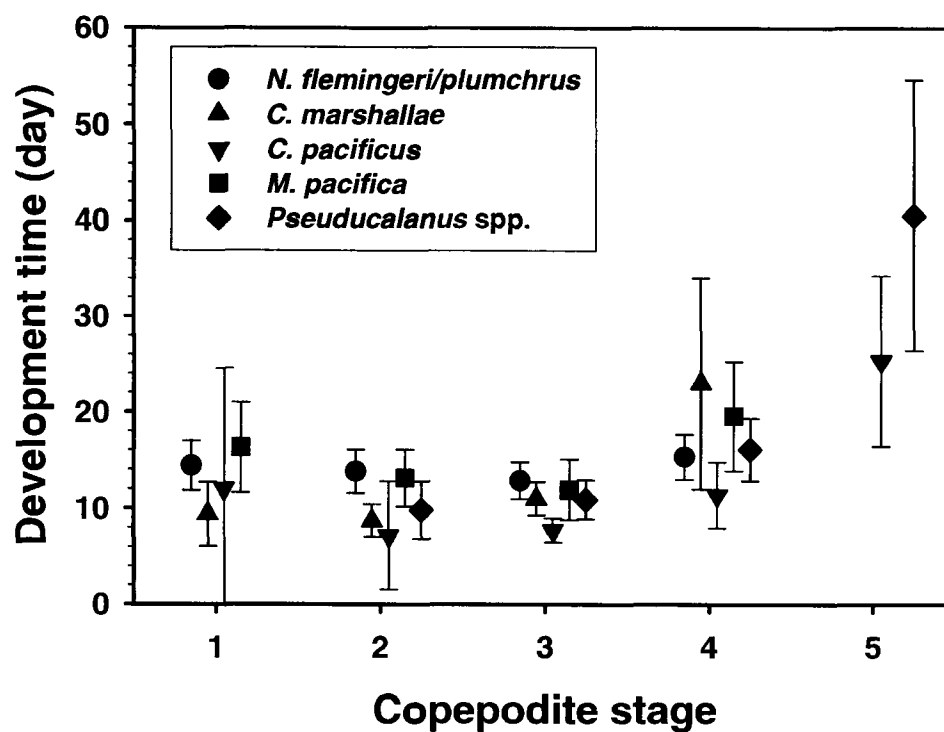


**Figure 4.6** Effect of temperature on growth rate and body size of *Pseudocalanus* spp. in the northern Gulf of Alaska 2002–2004.

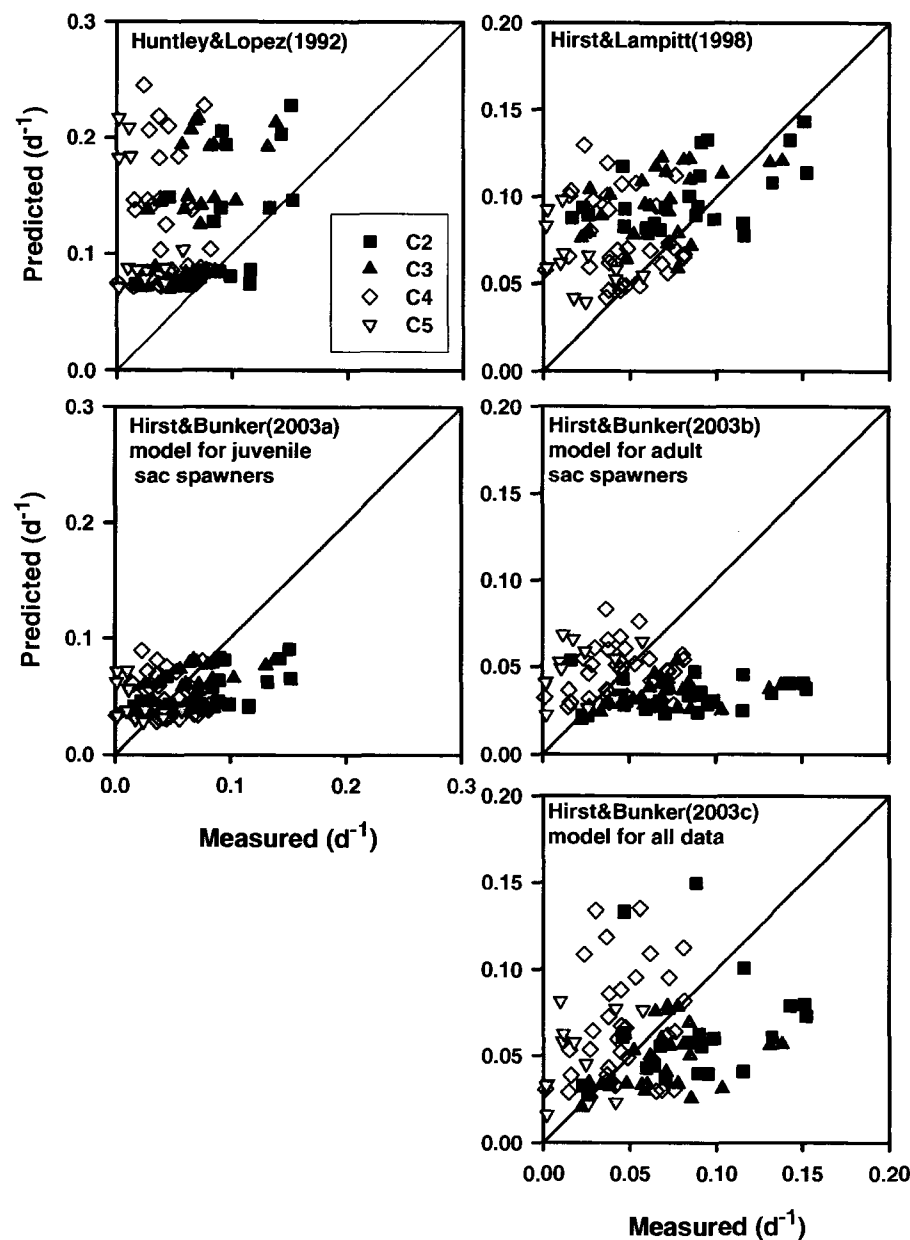




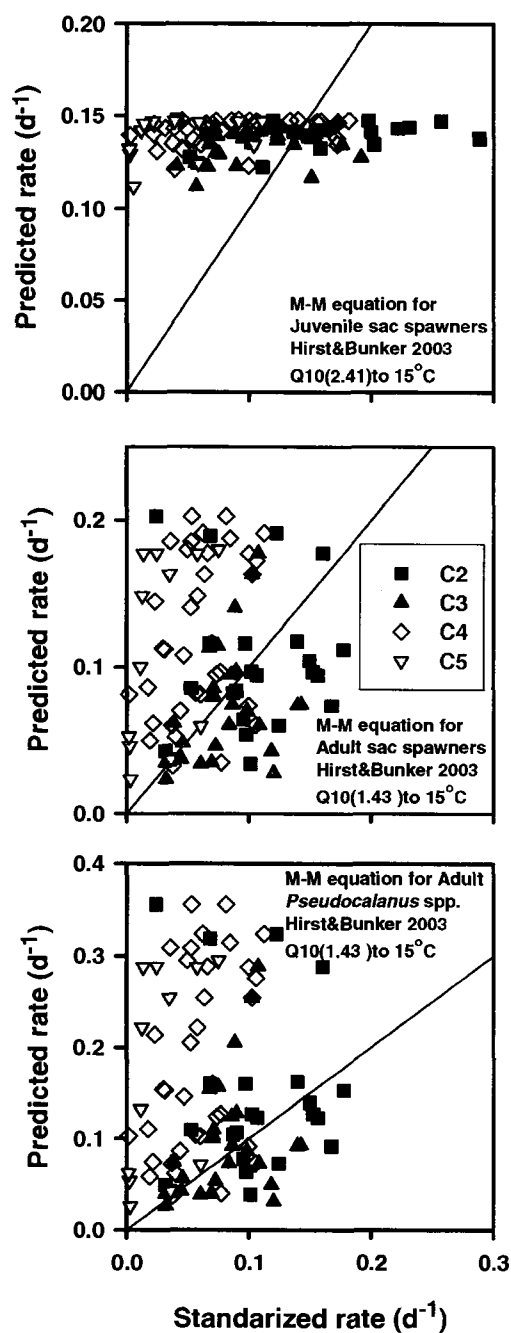
**Figure 4.7** Relationship between temperature-corrected growth rates, body size, and total chlorophyll  $a$  for *Pseudocalanus* spp. in the northern Gulf of Alaska 2002–2004.



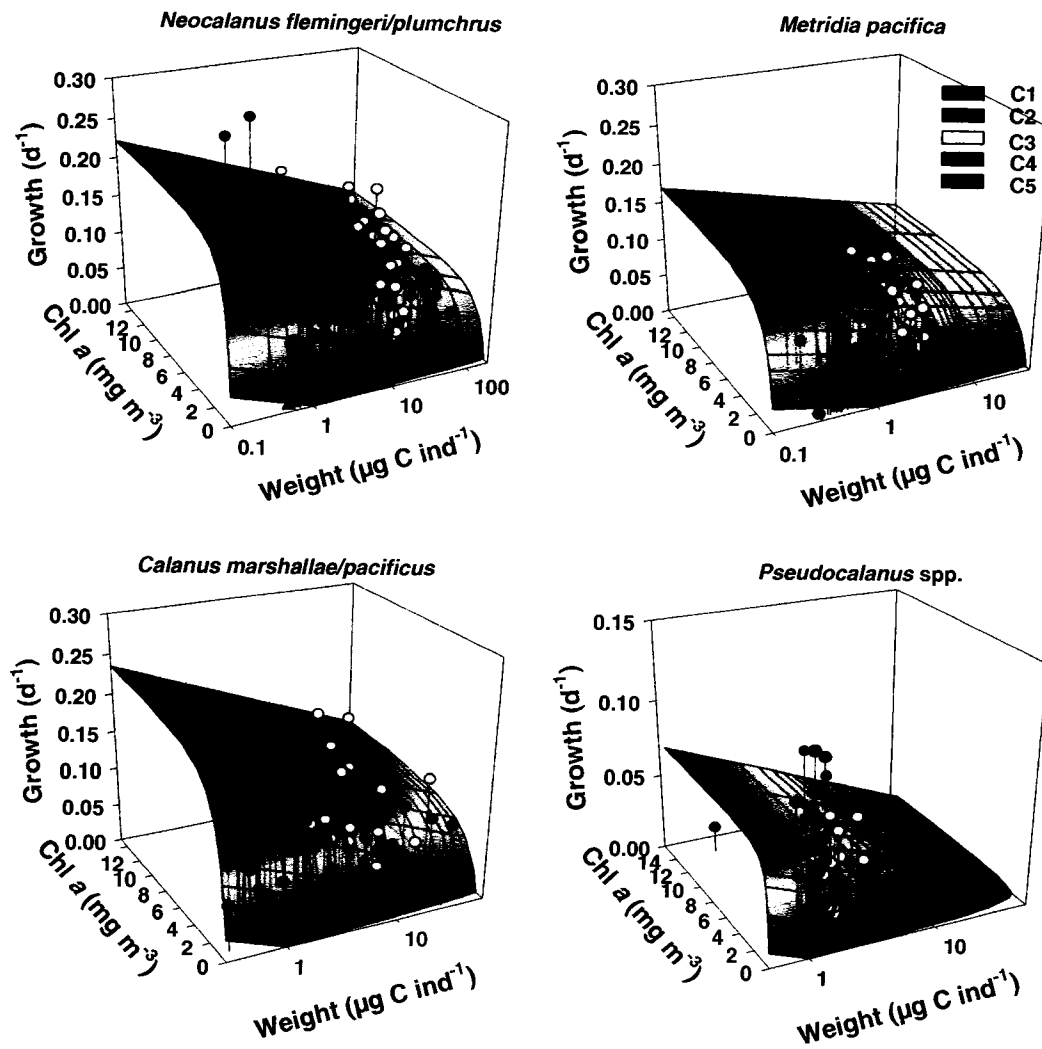
**Figure 4.8** Comparisons of the development time for the dominant copepods in the northern Gulf of Alaska. Data were corrected to 5°C using  $Q_{10}=2.7$ ; Error bars are 95% C.I.



**Figure 4.9** Comparisons of the measured growth rates for *Pseudocalanus* spp. and growth rates predicted from the models of Huntley and Lopez (1992), Hirst and Lampitt (1998), and Hirst and Bunker (2003). Hirst and Lampitt (1998) equation for all data equation (adults and juveniles of both broadcast and sac-spawners); Hirst and Bunker (2003) a: for juveniles broadcasters; b: for adult broadcasters; c: for all data combined.



**Figure 4.10** Comparisons of the temperature-corrected growth rates for *Pseudocalanus* spp. with the rates predicted from the three Michaelis-Menten relationships given for juvenile sac spawners, adult sac spawners and *Pseudocalanus* spp. by Hirst and Bunker (2003).



**Figure 4.11** Comparisons of the composite growth models at 5°C for dominant copepods in the northern Gulf of Alaska.

**Table 4.1** Temporal and spatial comparison of growth rates (SE, in parenthesis) (day<sup>-1</sup>) for *Pseudocalanus* spp. 2002–2004 in the northern Gulf of Alaska

Species	Temp (°C)	Growth rate (SE)						
		March	April	May	July	August	October	Average
<i>Pseudocalanus</i> spp.	4.2- 15.4	0.047 (0.009)	0.049 (0.005)	0.058 (0.006)	0.061 (0.011)	0.076 (0.019)	0.064 (0.009)	0.057 (0.004)

Species	Temp (°C)	Growth rate (SE)					
		PWS2	GAK1	GAK4	GAK9	GAK13	Average
<i>Pseudocalanus</i> spp.	4.2- 15.4	0.046 (0.006)	0.049 (0.006)	0.067 (0.008)	0.070 (0.011)	0.063 (0.009)	0.057 (0.004)

**Table 4.2** Growth rates ( $\text{day}^{-1}$ ) and development times (days, in parenthesis) for *Pseudocalanus* species in the subarctic Pacific and Oregon coast. \* corrected to these temperatures by  $Q_{10}$  of 2.7

Species	Temp (°C)	Growth rate and developmental time							Source
		C1	C2	C3	C4	C5	EPR	Average	
<i>Pseudocalanus</i> spp.	5*		0.063 (9.8)	0.044 (10.8)	0.036 (16.1)	0.020 (40.5)		0.042 (16.5)	This study
<i>Pseudocalanus</i> spp.	10*		0.103 (6.0)	0.073 (6.6)	0.060 (9.8)	0.034 (24.7)		0.070 (10.1)	This study
<i>Pseudocalanus</i> spp.	4		0.13 (4-5)	0.13 (4-5)	0.13 (4-5)	0.13 (4-5)		0.13 (4-5)	Vidal and Smith(1986)
<i>Pseudocalanus</i> <i>mimus</i>	11.8	0.22	0.22	0.22	0.22	0.22	0.06	0.22	Peterson <i>et al.</i> , (2002)

**Table 4.3** Relationships of *Pseudocalanus* spp. growth rate ( $Gr$ , day<sup>-1</sup>) to initial stage ( $Stg$ ), temperature ( $T$ , °C), chlorophyll  $a$  concentration ( $Chl$ , mg m<sup>-3</sup>), and body size ( $BW$ , µg C individual<sup>-1</sup>) in the northern Gulf of Alaska

Function	Equation	n	T (°C)	Coefficients ( <i>p</i> , partial <i>r</i> <sup>2</sup> )					<i>r</i> <sup>2</sup> ( <i>p</i> )
Multiple Regression	log <i>Gr</i> = <i>a</i> <sub>1</sub> + <i>a</i> <sub>2</sub> <i>Stg</i> + <i>a</i> <sub>3</sub> <i>T</i> + <i>a</i> <sub>4</sub> log <i>BW</i> + <i>a</i> <sub>5</sub> [Total <i>Chl</i> ] (C2–C5)	96	4.2-15.4	<i>a</i> <sub>1</sub>	<i>a</i> <sub>2</sub>	<i>a</i> <sub>3</sub>	<i>a</i> <sub>4</sub>	<i>a</i> <sub>5</sub>	0.3333 (<0.0001)
				-0.5855 (0.0002)	-0.3399 (<0.0001)	0.0209 (0.0437)	0.5385 (0.0220)	—	
					0.2354	0.0435	0.0558		
Total <i>Chl</i>				<i>a</i>	<i>b</i>	<i>g</i> <sub>max</sub>	<i>K</i> <sub>chl</sub>		
Michaelis-Menten	<i>g</i> = <i>Chl</i> [ <i>g</i> <sub>max</sub> ]/( <i>Chl</i> + <i>K</i> <sub>chl</sub> ) (C2–C5)	96	5			0.0456 (<0.0001)	0.0847 (0.380)		0.014 (0.2459)
	<i>g</i> = <i>Chl</i> [ <i>g</i> <sub>max</sub> ]/( <i>Chl</i> + <i>K</i> <sub>chl</sub> ) (C2–C5)	96	10			0.0749 (<0.0001)	0.0847 (0.380)		0.014 (0.2459)
Composite Nonlinear	<i>g</i> = <i>b</i> *log <i>BW</i> + <i>Chl</i> [ <i>g</i> <sub>max</sub> ]/( <i>Chl</i> + <i>K</i> <sub>chl</sub> ) (C2–C5)	96	5		-0.0313 (0.0015)	0.0636 (<0.0001)	0.1772 (0.0706)		0.117 (<0.0001)
	<i>g</i> = <i>b</i> *log <i>BW</i> + <i>Chl</i> [ <i>g</i> <sub>max</sub> ]/( <i>Chl</i> + <i>K</i> <sub>chl</sub> ) (C2–C5)	96	10		-0.0515 (0.0015)	0.1045 (<0.0001)	0.1772 (0.0706)		0.118 (<0.0001)
	<i>g</i> = <i>a</i> *stage+ <i>b</i> *log <i>BW</i> + <i>Chl</i> [ <i>g</i> <sub>max</sub> ]/( <i>Chl</i> + <i>K</i> <sub>chl</sub> ) (C2–C5)	96	5	-0.0241 (<0.0001)	0.0453 (0.0021)	0.1072 (<0.0001)	0.0097 (0.7076)		0.383 (<0.0001)
Chl >5 µm									
Michaelis-Menten	<i>g</i> = <i>Chl</i> [ <i>g</i> <sub>max</sub> ]/( <i>Chl</i> + <i>K</i> <sub>chl</sub> ) (C2–C5)	96	5			0.0482 (<0.0001)	0.0499 (0.101)		0.0541 (<0.0001)
	<i>g</i> = <i>Chl</i> [ <i>g</i> <sub>max</sub> ]/( <i>Chl</i> + <i>K</i> <sub>chl</sub> ) (C2–C5)	96	10			0.0792 (<0.0001)	0.0499 (0.101)		0.0546 (<0.0001)
Composite Nonlinear	<i>g</i> = <i>b</i> *log <i>BW</i> + <i>Chl</i> [ <i>g</i> <sub>max</sub> ]/( <i>Chl</i> + <i>K</i> <sub>chl</sub> ) (C2–C5)	96	5		-0.036 (0.00016)	0.067 (<0.0001)	0.074 (0.0055)		0.189 (<0.0001)
	<i>g</i> = <i>b</i> *log <i>BW</i> + <i>Chl</i> [ <i>g</i> <sub>max</sub> ]/( <i>Chl</i> + <i>K</i> <sub>chl</sub> ) (C2–C5)	96	10		-0.0587 (0.00016)	0.110 (<0.0001)	0.074 (0.0055)		0.190 (<0.0001)
	<i>g</i> = <i>a</i> *stage+ <i>b</i> *log <i>BW</i> + <i>Chl</i> [ <i>g</i> <sub>max</sub> ]/( <i>Chl</i> + <i>K</i> <sub>chl</sub> ) (C2–C5)	96	5	-0.0221 (<0.0001)	0.0361 (0.0139)	0.1069 (<0.0001)	0.0114 (0.1499)		0.400 (<0.0001)



**Table 4.4** Comparison of the  $Q_{10}$  standardized growth rate ( $\text{day}^{-1}$ ) of the dominant calanoid copepod species in the northern Gulf of Alaska during 2001–2004

Species	Temp (°C)	Growth rate	Egg production rate	Source
<i>Pseudocalanus</i> spp.	5.0	0.042		This study
<i>Calanus marshallae</i>	5.0	0.118		Liu and Hopcroft (in review)
<i>Calanus pacificus</i>	5.0	0.074		Liu and Hopcroft (in review)
<i>Metridia pacifica</i>	5.0	0.078		Liu and Hopcroft 2006b
<i>Metridia pacifica</i>	5.0		0.10	Hopcroft <i>et al.</i> , 2005
<i>Metridia okhotensis</i>	5.0		0.11	Hopcroft <i>et al.</i> , 2005
<i>Neocalanus flemingeri/plumchrus</i>	5.0	0.105		Liu and Hopcroft 2006a
<i>Centropages abdominalis</i>	5.0	0.141*		Slater and Hopcroft, 2005

\* Growth rate corrected from original 7.0°C to 5.0°C ( $Q_{10}=2.7$ ).

**Table 4.5** Comparison of growth rates predicted by global models with measured rates for *Pseudocalanus* spp. in the northern Gulf of Alaska

<i>Pseudocalanus</i> spp.		Percent of predicted to rates measured in this study					
Model	Temperature (°C)	C1	C2	C3	C4	C5	C2-C5
Huntley and Lopez, 1992	5.0-15.0		136%	201%	267%	589%	216%
Hirst and Lampitt, 1998	5.0-15.0		117%*	141%	168%	312%	150%
Hirst and Bunker, 2003 <sup>a</sup>	5.0-15.0		64%	85%*	107%*	216%	91%*
Hirst and Bunker, 2003 <sup>b</sup>	5.0-15.0		38%	49%	102%*	232%	70%
Hirst and Bunker, 2003 <sup>c</sup>	5.0-15.0		74%	70%	144%	237%	104%*
Hirst and Bunker, 2003 <sup>d</sup>	15.0		89%*	122%	162%	317%	134%
Hirst and Bunker, 2003 <sup>e</sup>	15.0		89%*	92%*	209%	402%	143%
Hirst and Bunker, 2003 <sup>f</sup>	15.0		124%*	122%*	316%	605%	208%

\* non-significant at  $\alpha=0.05$ , two sample, two tail t-Test assuming unequal variance.

In Hirst and Bunker (2003), a: for juvenile sac spawners; b: for adult sac spawners; c: for all data; d: Michaelis-Menten relationship for juvenile sac spawners at 15°C; e: Michaelis-Menten relationship for adult sac spawners at 15°C; f: Michaelis-Menten relationship for adult *Pseudocalanus* spp. at 15°C.

**Table 4.6** Comparison of the composite model for dominant copepods in the northern Gulf of Alaska during 2001–2004

Species	Temperature (°C)	Percent of predicted to measured rates					
		C1	C2	C3	C4	C5	C1–C5
<i>Neocalanus flemingeri/plumchrus</i>	5.0	131%	87%	87%	117%		98%
<i>Metridia pacifica</i>	5.0	109%	100%	87%	122%	303%*	105%
<i>Calanus marshallae/pacificus</i>	5.0	110%	87%	95%*	100%	169%	99%
<i>Pseudocalanus</i> spp.	5.0		82%	99%	109%	174%*	100%

\* significant at  $\alpha=0.05$ , two sample, two tail t-Test assuming unequal variance

## GENERAL CONCLUSIONS

This dissertation represents the first comprehensive study of growth characteristics of all the dominant copepods in the northern Gulf of Alaska. It addresses the growth and development rates of dominant copepod species in this area, thoroughly explores the functional responses of copepod growth rates to body size and environmental factors (i.e., temperature, chlorophyll *a*), considerably complements our knowledge on the roles of mesozooplankton in the flows of matter and energy in the dynamic marine ecosystem of the northern Gulf of Alaska, and finally challenges the generality of the existing global patterns of copepod growth for cold water species.

(1) The application of the artificial-cohort technique, and its modifications, has been successful in warm waters. This study is the first validation of this technique in cold waters. Although more variability is produced by this technique than by the single-stage method, ultimately it reveals the same underlying relationships to food resources (Chapter 1). The creation of a series of artificial cohorts that span the entire size range of the target zooplankton community provides growth data simultaneously on all the dominant species present in a collection (Chapters 1, 2, 3, 4). Furthermore, a significant attraction of this technique is that it can be routinely performed at sea. Thus, the artificial-cohort method appears to be the most practical method for local estimation of copepod community production. On the other hand, the single-stage method, while arguably superior, is only practical for larger species where stages may be more readily separated, requires more stable working conditions suitable for live sorting at sea, and requires significant manpower if more than one species is targeted simultaneously.

(2) Critical rate processes (i.e. growth rate and development time) addressed in this dissertation contribute to our existing understanding of the role of dominant copepod species in the marine ecosystem of the Gulf of Alaska (Chapters 1, 2, 3, 4). Typically, for broadcast calanoid species (i.e. *Neocalanus flemingeri/plumchrus*, *Metridia pacifica*, *Calanus marshallae*, and *C. pacificus*), their growth rates and development times are comparable (Chapters 1, 2, 3). Interestingly, although development times are comparable to other co-occurring calanoid copepods, growth rates of *Pseudocalanus* spp. are

considerably slower. Thus, the egg-carrying *Pseudocalanus* spp. appear to employ a life history strategy optimized for slow growth at low chlorophyll *a* concentration, that coincidentally keeps individuals relatively small, and may therefore reduce their susceptibility to visual predation (Chapter 4).

(3) Temperature strongly regulates the growth of copepods. In this area, the variability in thermal conditions exhibits a well-defined annual cycle, increasing in late spring, maximal in late summer and decreasing in fall. This cycle causes the weak correlation between temperature and growth rates for species abundantly occurring during the spring and early summer (Chapter 1). This temperature relationship appears to become more pronounced with the widening spectrum of temperature as the season progresses (Chapter 4). The interactive effects of temperature, food concentration and body size are confounded. Standardization of growth rates to a fixed temperature makes it feasible to reveal the underlying relationship between growth rates and the remnant factors (i.e., food concentrations, body size). After temperature standardization, growth rates are negatively related to developmental stages for all target species (Chapters 1, 2, 3, 4).

On large spatiotemporal scales, food limitation appears important in controlling the structure of marine ecosystems (Kiørboe, 1997; Hunt Jr. and McKinnell, 2006). In natural environments, growth of adult and juvenile copepods often tends to be food-limited (Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Hopcroft and Roff, 1998), and food limitation becomes more severe with increasing temperature (Hirst and Bunker, 2003). Thus, food-limitation is more pervasive in warm waters than in cold waters. Nonetheless, even in the Gulf of Alaska, the *in situ* growth of *N. flemingeri/plumchrus* appears to be generally food-limited compared to that seen in food enhancement experiments, with food-enriched effects dependent on the food items available and varying with developmental stage (Chapter 1). Food limited growth exists more commonly for other species, i.e., *M. pacifica*, *C. marshallae*, *C. pacificus*, *Pseudocalanus* spp., in this area, as many field values are below their saturated rates, especially for later developmental stages during summer and fall (Chapters 2, 3, 4). A similar finding also exists for *Centropages abdominalis* in this area (Slater and Hopcroft, 2005).

By far the most common measure of the food environment of copepods in aquatic ecosystems is chlorophyll *a*, although for some species it may be a poor predictor of growth and fecundity (Hirst and Bunker, 2003; Bunker and Hirst, 2004). For the target species in this study, however, chlorophyll *a* is generally a significant predictor of growth rates (Chapters 1, 2, 3, 4). With the progression of ontogenetic development, copepods encounter increased availability and variety of food items, and this in conjunction with food-limited growth undoubtedly accounts for the various degrees of scatter in the response of growth to chlorophyll *a*, which most likely develops at lower chlorophyll concentrations outside the spring bloom in this area (Chapters 2, 3). Moreover, the low explanatory power of chlorophyll *a* for *Pseudocalanus* growth rates (Chapter 4), supports the hypothesis that juvenile growth rates of egg-carrying copepods tend to depend more heavily on temperature rather than food, in contrast to those of broadcast species (Hirst and Bunker, 2003).

Globally, rates of copepod growth are negatively correlated with body size (Hirst and Bunker, 2003). This size-dependent growth pattern exists for all target species in this study (Chapters 1, 2, 3, 4), because the severity of food-limited growth increases with body sizes (Vidal, 1980; Hopcroft *et al.*, 1998; McKinnon, 1996; Hirst and Bunker, 2003). This study is the first attempt to explore this stage-dependent relationship in the field. Surprisingly, after removing temperature effects, the positive relationship between growth rate and body size within a single copepodite stage is clearly observed by the single stage method (Chapter 1). Under favorable food conditions, animals within a stage that are growing rapidly tend to be larger in size than those growing slowly. While similar patterns are observed for other target species, patterns tend to become blurred (Chapters 2, 3, 4). The relatively constant temperature and optimal food conditions during spring make this pattern most clear for *Neocalanus* species. However, seasonally varying temperature and food conditions experienced by other species, as well as the lack of pure stages produced by the artificial-cohort method, blur this pattern. Thus, based on this study it is reasonable to believe that the within stage pattern exists in general for marine copepods in the field.

(4) One objective in this study was to test the utility of global models currently used for predicting growth rates of copepods. Comparisons of measured rates with the predicted rates by models indicate notable errors (Chapters 1, 2, 3, 4). The lack of predictive power of these models is not surprising considering that these empirical equations were developed using limited data on species living in cold waters, especially for juvenile somatic growth, and virtually no data from the subarctic Pacific. Globally, predictive models are necessary to estimate growth, and hence secondary production, over large spatial and temporal scales. Therefore, there is a constant need to test and refine such models by comparing them with new rates from various ecosystem types.

Recent attempts to determine “global models” uncover a significant Michaelis-Menten relationship between chlorophyll *a* and growth rates of copepods after removing temperature effects (Hirst and Bunker, 2003). However, synergistic effects between chlorophyll *a* and body size still confound the growth rate of copepods, as revealed by the composite nonlinear model first developed for *Metridia pacifica* incorporating body size into the traditional Michaelis-Menten function (Chapter 2), and then successfully employed for other species (Chapters 3, 4). Fitting this model improves the explainable variance in growth rates (Chapters 2, 3, 4). Explanatory power for the variability in growth rate increased with the spectrum of body size and range of chlorophyll *a* concentrations, i.e., synergistic effects of food condition and body size tend to be more pronounced as these ranges widen, particularly for food conditions (Chapter 3). Interestingly, despite their different geographic ranges, growth rates of *Calanus marshallae* and *C. pacificus* appear to have similar functional responses to chlorophyll *a*, and body size, with tempo-spatial differences in occurrence responsible for apparent differences in mean rates (Chapter 3). More broadly, the fitted composite model for species within the family Calanidae (i.e. *Neocalanus flemingeri/plumchrus* and *Calanus marshallae/pacificus*) is still significant, and even holds well with the inclusion of *Metridia pacifica* (family Metridinidae) from this area, suggesting it might create a predictive foundation for other broadcasting species in this area and similar subpolar environments.

As one of the key issues in marine zooplankton research, studying the relationships between growth and environmental conditions is required to construct global patterns of production (Paffenhöfer *et al.*, 2001), and this study makes new contributions to that goal. Basic research yielding direct measurements of copepod growth rates is still needed, especially for ecosystems currently lacking this kind of information. Significant errors in estimating secondary production arising from the use of biased growth data and/or inappropriate models could have large consequences in quantifying the linkage of copepods to both higher and lower trophic levels, and how this might be altered by short-term and long-term climate change. Future research in this field should continue to work in even colder waters (e.g., the Arctic, Antarctic and their adjacent waters) to refine the existing knowledge of global patterns on zooplankton growth.

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